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PÉTER MELIUS JUHÁSZ (1536?—1572)

Von

R. Soó

Botanischer Garten der L. Eötvös Universität, Budapest

(Eingegangen am 10. November 1971)

In memoriam of P. M. J., on the occasion of the 400th anniversary of his death. His book (Herbarium . . . 1572) is the first herbal in Hungarian, mainly after *Lonicerus*, and also the first Hungarian agricultural and medical work. In the sixteenth century P. M. J. was one of the most renowned Calvinist missionaries, bishop of the town Debrecen.

Die Anfänge der ungarischen Botanik, die ersten Forschungen über die artenreiche ungarische Flora weisen nach der Stadt Debrecen. Debreziner Fundortsangaben liefern die ersten genaueren Unterlagen für die Erschliessung der Pflanzenwelt Ungarns; solcherlei Informationen findet man jedenfalls im ersten ungarischen Werk aus dem Gebiete der Botanik (zugleich auch die Medizin und Landwirtschaft) im postumen Werk »Herbarium« des grossen Reformators und überhaupt eines der hervorragendsten Vertreter des ungarischen Geisteslebens im 16. Jahrhundert PÉTER MELIUS JUHÁSZ. Der volle Titel lautet: »Herbarium. Az Fáknac Füveknec nevekről, természetekről és hasznairól. Magyar nyelvre, és ez rendre hoszta az Doctoroc Könyueiből az HORHI MELIUS PETER. Nyomtattot Colosuárat HELTAI GASPÁRNE Mühellyébé, 1.5.78. Esztendőben.) (zu deutsch etwa: »Herbarium. Über Namen, Natur und Nutzen der Bäume und Kräuter. In ungarische Sprache gefasst und solcherweis angeordnet aus der Doctores Büchern, von PETRUS MELIUS aus HORHI. Gedruckt zu Klausenburg in der Offizin der Frau GÁSPÁR HELTAI im Jahre 1578. 188 Blätter in Kleinoktav«). (Die dem Textteil vorangehenden Verzeichnisse der lateinischen, ungarischen und deutschen Pflanzennamen sowie der Krankheiten sind mit Versalien paginiert).

Der sprachgewaltige Prediger der Reformation und Bischof von Debrecen, dessen unerschütterliche Glaubensstärke und Überzeugung, umfassendes Wissen, hervorragende Organisationsgabe und eiserner Wille diese Stadt zum »kalvinistischen Rom« der Ungarn machte, ja ihm selbst von seinen Gegnern den Spottnamen »Papst Petrus« eintrug; dessen Grösse und Wirken »aere perennius« seine Bücher verkünden — dieser Mann hatte inmitten seiner zermürbenden Kämpfe noch dazu Lust und Zeit gefunden, dem einfachen Volk auch in seinen leiblichen Nöten heilenden Rat zu spenden. Das Kräuterbuch MELIUS' ist im Grunde ein volkstümlicher medizinischer Ratgeber, ein Wegweiser zur arzneimässigen Verwendung der angeführten Pflanzen.

Mit dem Naturalismus der Renaissance setzte damals auch in der Botanik eine neue Epoche ein. Das Geisteskraut des primitiven Pflanzenkults, die phantastischen und mythischen Gebilde der Hortus Sanitatis, mitsamt dem ganzen Rattenschwanz des abergläubischen Beiwerkes, der magischen Vorstellungen, Sagen und Legenden wurden von den grösstenteils in Latein oder Deutsch verfassten, neuen Ärztebotaniken — betitelt gewöhnlich als »Herbarius« oder »Kräuterbuch« — verdrängt; diese enthalten, dem Formkult jener Zeit folgend, immer genauere Beschreibungen, immer naturgetreuere und kunstvollere Bilder — hatte doch die Pflanzenzeichnung, besonders die Kunst des Holzstichs im Jahrhundert DÜRERs ihren Höhenpunkt erreicht —, wobei es auch nicht unterlassen wird, die heilkräftigen bzw. schädlichen Wirkungen der einzelnen Pflanzen eingehend, jedoch auch schon mit einiger Kritik zu behandeln. Diese Kräuterbücher — vor allem jenes des LONICERUS — dienten MELIUS als Quellenwerke; von der Wissenschaftsgeschichte her mögen sie ja bloss als ungarische Übersetzungen gelten, immerhin ist MELIUS doch als erster anzusehen, der sich in Ungarn mit Botanik und Medizin befasste.

PÉTER JUHÁSZ »MELIUS« wurde in den dreissiger Jahren des 16. Jahrhunderts (vermutlich 1536) in einem später untergegangenen Dorf Namens Horhi (Komitat Somogy) geboren. (Das ergäbe insgesamt nur 36 Lebensjahre für sein ganzes Schaffen: für die Abfassung seiner zahlreichen Schriften, für die Disputen, für das ganze bedeutende gesellschaftliche und politische Wirken, eine fast unglaublich kurz erscheinende Zeit). Über seine Herkunft und Jugendjahre ist nichts bekannt. MELIUS (latinisierte Form des griechischen »meleios« für »JUHÁSZ-SCHÄFER«) ist ein nach humanistischer Mode angenommener Name. In den Jahren 1553—54 besuchte er die Schule in Tolna, der Herbst 1556 findet ihn an der Universität zu Wittenberg — wo er wohl die Kräuterbücher kennen lernte und auch deren Übersetzung in Angriff genommen haben dürfte — i. J. 1558 wird er von JÁNOS ENYINGI TÖRÖK als Geistlicher nach Debrecen berufen, wo er auch von der Bürgerschaft zum Stadtpfarrer, und alsbald zum Bischof gewählt wird. Er lenkt nun das kirchliche und gesellschaftliche Leben dieser feudal-bürgerlichen Stadt; ihm ist es zuzuschreiben, dass die Ungarische Tiefebene und auch das ungarisch besiedelte Siebenbürgen inmitten der Stürme der Reformation grösstenteils kalvinistisch wurde. Die Lehren der katholischen Kirche bekämpfte er zeitlebens mit einem wahren Fanatismus; ihre Priester und Institutionen zieh er geistiger Buhlerei und Unzucht, wobei er sie für die leibliche Unzucht mit Kraftausdrücken gröbster Art beschimpft (BÁN). Allerdings nicht minder unbändig wütet er auch gegen die anderen protestantischen Bekenntnisse, wie gegen die Lutheraner, besonders aber gegen die Antitrinitarier oder Unitarier, die damals in Siebenbürgen starken Anhang fanden. So streitet er viel mit FERENC DÁVID, dem Oberhaupt dieser Konfession (u. a. 1569 in Grosswardein in der Anwesenheit

des Fürsten von Siebenbürgen, JÁNOS ZSIGMOND, von dem er sich eben aus diesem Grunde Tadel zuzog). Von blindem Eifer, und in seiner Überzeugung unbeirrbar, gab er sich nie geschlagen — er war gewiss ein starrer Dogmatiker — doch solcherart gelang es ihm die reformierte Kirche Ungarns zu retten, ja sogar zu festigen. Im Laufe von elf Jahren liess er insgesamt 28 Schriften drucken: Glaubensbekenntnisse, Kathekismen in Latein und Ungarisch, theologische Disputationen, Predigten, die sich heute allerdings nicht eben leicht lesen lassen. Seine Bibelübersetzungen sind verlorengegangen; der dauernhafteste Teil seines literarischen Schaffens ist daher das Herbarium geworden.

Wir wissen nicht, ob das Manuskript im Nachlass MELIUS' schon in fertiger Fassung vorhanden war, oder ob es erst vom Herausgeber, aus verschiedenen Schriften zusammengestellt worden ist (wie dies NATTER-NÁD vermutet). Vielleicht hatte es MELIUS in vier Abschnitten verfasst. Die Kapitel werden immer umfangreicher, und während man anfangs fast wörtliche Übersetzungen aus dem Naturalis Historiae opus novum von LONICERUS (I—II, Frankfurt, 1551, 1555), hauptsächlich aber aus dessen Kräuterbuch findet (Frankfurt, zahlreiche Auflagen seit 1557; GOMBOCZ wählte die Ausgabe 1569 zum Vergleich), werden doch im weiteren auch andere Autoren zitiert. Eigentlich ist das Herbarium unvollendet geblieben. Es umfasst 232 Kapitel mit etwa 620 Pflanzenarten bzw. etwa 2000 Pflanzennamen, wogegen das »Kräuterbuch« 419 »Capitel« hatte. Ganz gewiss benutzte er von den verschiedenen Kräuterbüchern seiner Zeit jene von FUCHS, MATTHIOLUS und BOCK (TRAGUS); manchmal kritisierte er sie auch (z. B. pp. 59a, 80a, 182a, 187a), mitunter nimmt er auch entschieden Stellung gegen manche falsche Überlieferungen, alte Aberglauben. Eine Stelle aus PLINIUS bezeichnet er als »falsches Götzentum wider Gott«. Auch er selbst botanisierte; es werden bei mehreren Pflanzen die Fundorte in der Nyírség (»Nyíri föld«) und der Umgebung von Debrecen (»Csere«, »Fancsika«, »Bedőháza«, »Malomgát«, »Pércs« usw.) angeführt, dies wären die ersten floristischen Angaben aus Ungarn. Sogar die Heilanzeigen hatte MELIUS zum Teil an sich selber erprobt (»Erprobtes Ding«). Zwar hat er zahlreiche, auch in Ungarn unbekannte Arten von LONICERUS übernommen, viele ähnliche oder einander nahestehende Arten und Gattungen verwechselt, unterschiedliche zusammengelegt, gleiche Fehler kommen auch in anderen damaligen Kräuterbüchern vor. Jedes Kapitel (z. B. De Menta) bringt die lateinischen, ungarischen und deutschen Namen der besprochenen Arten, manchmal auch gewisse Kennzeichen; wenn mehrere Pflanzen behandelt werden, sind deren Unterscheidungsmerkmale angegeben, seltener auch Daten über ihre Vorkommen. Danach folgen unter der Überschrift »Természeti« (etwa: »Deren Natur«) gemäss des damaligen Humoralsystems die Angabe der feuchtigenden, trocknenden, wärmenden oder kühlenden Wirkung der Pflanze, unter dem Titel »Belső hasznai« (»Innerer Nutzen«) die Indikationen

für den oralen Gebrauch als Medikament, unter »Külső hasznai« (»Äusserer Nutzen«) die Möglichkeiten der äusserlichen Anwendung.

Abschliessend gibt es in einigen Kapiteln noch Rezepte zur Bereitung irgendeines Öls, Sirups u. dgl. aus der betreffenden Pflanze. Am Anfang des Werkes werden — ziemlich knapp — die Holzpflanzen behandelt, während innerhalb dieses Teils — doch nur in einigen Kapiteln — die Pilze (De Fungis) und die Moose (De Musco) Erwähnung finden. Den grössten Teil des Buches nehmen die »Namen und Eigenschaften der Kräuter« d. h. der krautigen Blütenpflanzen ein (»A fueknek nevekről és természetekről«), hingegen werden (im Kapitel »De Gramine«) die Seggen äusserst kurz gestreift. Neben den vielen ärztlichen — mitunter wohl etwas quacksalberischen — Rezepten findet man vielfach auch sonstige praktische Ratschläge, so u.a. zur richtigen Weinpflege, zur Fleischkonservierung, zur Bekämpfung der Schweinepest, zur Vertilgung von Ungeziefer (Wanzen, Läusen, Fliegen) sowie Ratten, Mäusen und Fledermäusen, probate Mittel gegen Bienenstiche wie gegen Glatzköpfigkeit, ja sogar über die Herstellung von Tinte oder über das Ausmalen von Büchern erfährt man Wissenswertes. Es ist auffallend, dass gegen ein und dieselbe Krankheit oft ganz verschiedene Pflanzen empfohlen werden; die freilich nach unserem heutigen Wissen ohne jeglichen Wert sind. Stellenweise übernimmt er auch allerhand naturhistorische Märchen antiker Autoren. Immerhin, sehr viele der von ihm identifizierten Pflanzen wurden noch im vergangenen Jahrhundert zumindest in der Volksmedizin benutzt; an die 140 sind auch gegenwärtig als einheimische Heilpflanzen bekannt, ja 52 davon sind sogar in der amtlichen ungarischen Pharmakopaea verzeichnet. Nach HALMAI finden sich 72,6% unserer ganzen Offizinalflora schon im Herbarium, wenn auch nicht alle mit ihrer heutigen Rolle und Bedeutung.

Zusätzlich bietet MELIUS noch wertvolles Material zur Geschichte der Krankheitsbezeichnungen im Ungarischen. So z. B. »francu«: Syphilis, »ránt«: Milzgeschwulst, »rothasztó feneseb« : Krebs, »tárgy« : Geschwür, Schwäre, »mérges köves kelés« : Furunkel usw.; hie und da schildert er auch die Symptome je einer Krankheit.

Die MELIUS-Studie L. FIALKOWSKIS (1885) ist verlorengegangen, so blieb die Identifizierung der MELIUSschen Namen mit der heute gültigen Nomenklatur E. GOMBOCZ vorbehalten (1936), was bei 394 Arten mit annähernder Sicherheit gelungen ist. NATTER-NÁD (1962) führt ergänzungsweise aber wissenschaftlich unbegründet weitere Namen auf, die alle unzuverlässig oder gar irrig sind (manchmal noch dazu in falscher Schreibweise); man merkt, dass kein Fachmann am Werke war.

Als grösstes Verdienst ist jedoch dem Herbarium die Bewahrung von etwa 2000 alten ungarischen Pflanzennamen anzurechnen; auf diesem Gebiet stellt dieses Werk neben der um die Mitte des 16. Jahrhunderts verfassten, aber erst 1590 herausgegebenen »Nomenclatura« des BALÁZS SZIKSZAI FABRI-

CIUS das wichtigste Quellenwerk dar. Leider sind viele dieser kernigen Ausdrücke im Zuge der ungarischen sog. »Spracherneuerung« des 19. Jahrhundert den gekünstelten Wortgebilden der offiziellen Wissenschaft zum Opfer gefallen. Für den Wert und die Brauchbarkeit des Werkes spricht jedenfalls, dass mehrere Nachahmer, ja Plagiatoren gefunden hat, so ist das »Füves könyv« des ANDRÁS BEYTHE (Németújvár) (heute: Güssing, Bgld.) (1595) teilweise eine Übersetzung von MATTHIOLUS, grösseren Teils aber eine Abschrift der MELIUSschen Arbeit.

Die grosse Bibliographie PRITZELS (ed. 2, 1872: 159) führt das MELIUSsche Kräuterbuch unter dem Verfassernamen »JUHÁSZ vel IHÁSZ«, hingegen mit falscher Titelangabe an; hier wird (FRANZ ALEXIUS) HORÁNYI erwähnt, der in seinem literaturgeschichtlichen Werk »Memoria Hungarorum« (1775—77) über eine Debreziner Ausgabe des Herbariums aus dem Jahre 1562 berichtet hätte, was jedoch nicht zutrifft. PRITZEL zitiert ferner das einzige tschechische Kräuterbuch aus dem 16. Jahrhundert u. zw. die Übersetzung des klassischen Werkes von MATTHIOLUS (Commentarii ad Dioscuridem . . .), mit wunderschönen, naturgetreuen Holzstichen in Kleinfolio. Dieses Werk erlebte zwei Auflagen unter dem Titel »Herbarz: ginak Bylinarz . . .« die erste 1562 bei THADDEUS HAGEK, die zweite 1566 im Verlag von ADEM HUBER und DANIEL ADAM (beide in Prag). Die erste enthält — wie aus dem in meinem Besitz befindlichen Exemplar auch ersichtlich — den tschechischen, lateinischen und deutschen Namen jeder Pflanze, samt Abbildung kurzer Beschreibung und Angabe der medizinischen Belange. Von etwaigen Kräuterbüchern gleichen Alters aus den anderen volksdemokratischen Ländern ist mir nichts bekannt.*

MELIUS selbst konnte sein Herbarium nicht mehr herausgeben. Dieser Aufgabe hatte sich dann die Witwe GÁSPÁR HELTAIS angenommen. Meine Erinnerung anlässlich der vierten Jahrhundertwende seines Todes möchte ich mit einigen Zeilen aus der Vorrede zur genannten Ausgabe schliessen: »Ezen dologban törte fejét a mi időnkben a bölcs férfiu, MELIUS PÉTER Döbrötzeni keresztyén egyház Pásztora. Közönséges betegségekről való orvosságoknak összeszedegetésében és Magyar nyelvre fordításában munkálkodott. Azért az irása és külömb-külömbféle bölcs Orvosoknak könyvéből egybeszedése és fáradsága a Jámboré volt, a kinyomtatásnak munkája és költsége enyim. Ezt éntőlem ilyen szegény özvegy asszontól a Magyar nemzet jó néven vegye.« (In deutscher Übertragung etwa: »Mit solchen Dingen trug sich zu unserer Zeit der weise Mann PETER MELIUS, Hirte der christlichen Kirche zu Döbrötzen.

* Von den rund ein Dutzend erhalten geblieben bzw. bekannten exemplaren des MELIUS-Buches besitze ich selbst eines (das allerdings nicht ganz vollständig ist): ferner verschiedene Ausgaben der ervähnten Kräuterbücher von FUCHS, MATTHIOLUS, BOCK, an Inkunabeln den Hortus sanitatis minor, 1493 (nur mit den Beschreibungen und Holsstichen der Pflanzen), sowie den Hortus sanitatis major, 1947, der aber auch die Tiere und Mineralien behandelt.

Er befleissigte sich mit dem Zusammenlesen von Arzneien für die gemeinen Krankheiten und mit deren Übersetzung in die Ungarische Sprache. Also war auch der Niederschrift und des Zusammenklaubens aus den Büchern gar vieler weiser Ärzte Mühe des Frommen Mannes, die Arbeit und alle Kosten des Druckes die meinigen. Dies möge die Ungarische Nation mir, armer Witfrau zum Verdienst anrechnen.«

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MOUSSES AFRICAINES RÉCOLTÉES PAR M. DÉNES BALÁZS

Par

M. BIZOT[1]

(Reçu le 10 June 1971)

In the course of an extensive African journey through Algeria and the Cameroons as well as Kenya and Ethiopia, Dr. BALÁZS, Hungarian geographer, assembled a copious collection of Bryophytes. Doctor PÓCS (Teacher's Training College, Eger, Hungary) asked me to study the material.

A study of the abundant material permitted the description of a great many new species and varieties: *Acanthocladium Cuynetii, Acroporium Pocsii, Didymodon rigidulus* var. *acutus, Fabronia Pocsii, Fabronia Pocsii* var. *cameruniae, Fissidens Cuynetii, Hookeriopsis, Balazsii, Leptodontium* (?) *Allorgei, Pogonatum afrournigerum, Rhynchostegium Jovet-Astii, Tortula Pierrotii, Tortula ruralis* var. *subpapillosissima, Tortula Toutonii.*

It was possible to establish the presence of species with a remote origin, e.g. *Thuidium borbonicum*, and to recognize the synonymic identity of diverse species, e.g. *Stereophyllum radiculosum* with *Stereophyllum indicum* as well as that of *Stereophyllum nitens* with diverse African species. Besides, Dr BALÁZS had occasion to collect fructifying *Fissidens subarboreus*, so we can confirm POTIER DE LA VARDE's concepts concerning the genus *Monkemeyera.* Characterized by a peristome of whole teeth it is linked by insensible transitions to the genus Fissidens with peristomial teeth bifurcating beyond the middle.

Au cours d'un long voyage en Afrique qui l'a conduit d'Algérie au Cameroun, puis au Kenya et en Ethiopie, M. D. BALÁZS, géographe hongrois a fait de copieuses récoltes de Bryophytes M. T. PÓCS, de l'Institut Pédagogique d'Eger m'en a confié l'étude.

L'itinéraire de son voyage est représenté sur les cartes où seront mentionnées les diverses localités où ont été faites les récoltes.

Au lieu de présenter le catalogue des espèces sous la forme systématique, il nous semble préférable de les grouper suivant les points de récoltes, afin de donner une idée des assocations qui existent en Afrique. Quelques remarques critiques de certaines espèces termineront chaque énumération.

Les listes seront données en suivant l'ordre systématique de BROTHERUS [11] en utilisant la nomenclature reconnue par l'Index [25].

[1] Laboratoire de Botanique et de Cryptogamie de la Faculté des Sciences Pharmaceutiques et Biologiques de Dijon.

Fig. 1
Localités des collectionnements du M. D. BALÁZS

Carte A) Afrique du Nord

1. Djebel Ressas, Tunésie, 10. 2. 1967. 2. Djebel Oust, Tunésie, 11. 2. 1967. — 3. Thuburbo Majus près Pont du Fahs, Tunésie, 12. 2. 1967. — 4. Dougga, Tunésie, 12. 2. 1967. — 5. Maktar (Mactaris), Tunésie, 12. 2. 1967. — 6. Qued Seldja près Tozeur, Tunésie, 20. 2. 1967. — 7. Timgad près Batna, Mts. Aurés, Algérie, 26. 2. 1967. — 8. Djebel Belezma près Batna, Algérie, 27. 2. 1967. — 9. Fontaine Chaude près Batna, Algérie, 28. 2. 1967. — 10. Oase El Golea, Algérie, 12. 3. 1967. — 11. Leptis Magna près Tripolis, Libye.

Afrique du Nord

Les déterminations on tété faites en collaboration avec M. R. B. PIERROT que je remercie de son aide amicale.

Algérie: — Sur les pierres et la terre des ruines de Timgad (n° 83 et 119)

Pleurochaete squarrosa (Brid.) Lindb., *Didymodon rigidulus* Hedw., *Barbula cylindrica* (Tayl.) Schpr., *Aloina rigida* (Hedw.) Limpr. var. *ambigua* (B. S. G.) Craig., *Tortula Vahliana* (Schultz.) Mont., *Grimmia orbicularis* Bruch., *Bryum bicolor* Dicks., *B. torquescens* Bruch.

— Sur la terre argileuse à El Golea (n° 122):

Bryum radiculosum Brid.

— Rochers calcaires près de la Fontaine Chaude à 30 km nord-est de Batna (n° 121):

Pleurochaete squarrosa (Brid.) Lindb., *Didymodon rigidulus* Hedw., *D. revoluta* Brid., *Tortula ruralis* (Hedw.) G. M. S. var. *subpapillosissima* Biz. et Pier., *Grimmia orbicularis* Bruch., *Bryum radiculosum* Brid.

— Dans une forêt de Cèdres sur les troncs et les rochers au Djebel Belezma à 15 km. à l'ouest de Batna (N° 120):

Dicranoweisia cirrhata (Hedw.) Lindb., *Bryoerythrophyllum recurvirostre* (Hedw.) Chen., *Barbula fallax*: Hedw., *Tortula subulata* Hedw. var. *angustata* (Wils.) Limpr., *T. inermis* (Brid.) Mont., *T. intermedia* (Brid.) de Not., *T. ruralis* (Hedw.) G. M. S. sub. *papillosissima* Biz. et Pier., *Grimmia pulvinata* (Hedw.) Sm., *G. ovalis* (Hedw.) Lindb., *Bryum capillare* Hedw.
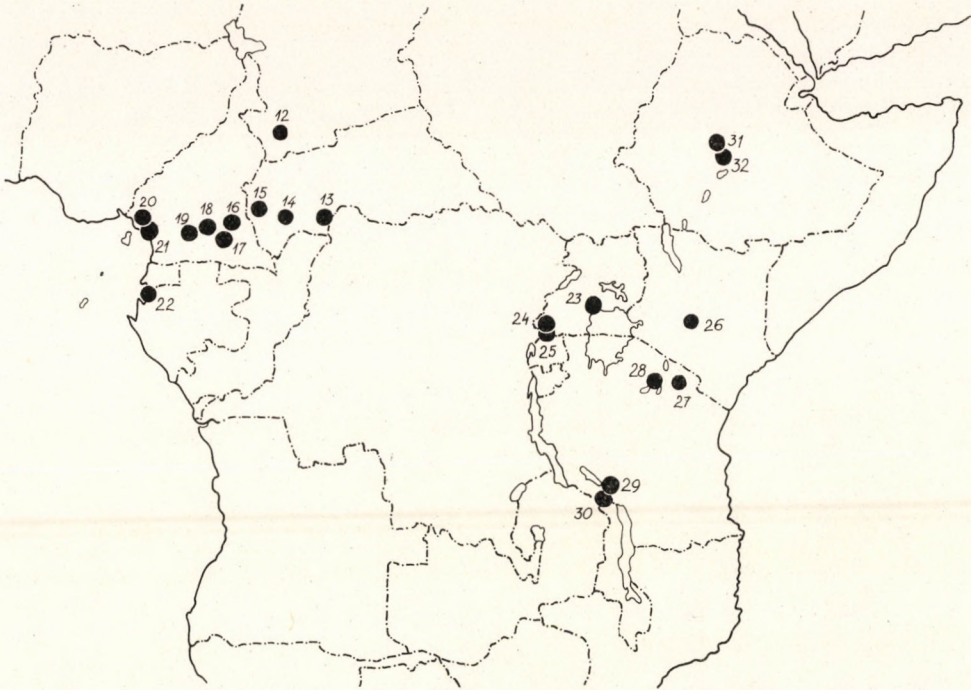
Fig. 2

Carte B) Afrique tropicale

12. Bebo, Sud Chad, 3. 6. 1967. — 13. Bangui, Rép. Centraficaine, 10. 6. 1967. — 14. Yaloké, Rép. Centrafricaine, 18. 6. 1967. — 15. Bouar, Rép. Centrafricaine, 19. 6. 1967. — 16. Ndokayo, Cameroun, 20. 6. 1967. — 17. Bertoua, Cameroun, 22. 6. 1967. — 18. Casca des Nachtigal au rivière Sanaga, Cameroun, 24. 6. 1967. — 19. Yaoundé, Cameroun, 26. 6 1967. — 20. Douala, Cameroun, 5. 7. 1967. — 21. Kumba. Lac Barombi-Mbo et Mt. Cameroun, Cameroun, 6. 8. 1967 et 25—27. 11. 1967. — 22. Libreville et Owendo, Gabon, 10—15. 11. 1967. — 23. Kisoro, Traveller's Rest, Uganda, 20. 12. 1967. — 24. Mafuga Forest, Kigezi District, Uganda, 22. 12. 1967. — 25. Moutozho, Ankole District, Uganda, 22. 12. 1967. — 26. Mt. Kenya, Kenya, 19—20. 1. 1968. — 27. Mt. Meru, Tanzanie, 29. 1. 1968. — 28. Crater du Ngorongoro, 2. 2. 1968. Tanzanie. — 29. Mts. Mbeya, Tanzanie, 7. 2. 1968. — 30. Natural Bridge près Lugombo, Rungwe Distric, Tanzanie, 9. 2. 1968. — 31. et 32. Lac Debre Zeit près Addis Abeba, Ethiopie, 9. 3. 1968.

var. *flaccidum* (Brid.) B. S. G., *B. radiculosum* Brid., *Orthotrichum rupestre* Schwaegr., *O. anomalum* (Hedw., *O. speciosum* Nees., *Pterygynandrum filiforme* Hedw., *P. filiforme* var. *majus* (de Not.) de Not. *Homalothecium algerianum* Besch., *Brachythecium velutinum* (Hedw.) B. S. G.

Tunisie: — Rochers frais ombragés à Qued Seldja 15 km nord-ouest de Metkabni (n° 117):

Grimmia Mairei Card. et Copp.

— Sur les pierres des ruines de Maktar (n° 115):

Didymodon rigidulus Hedw., *Aloinarigida* (Hedw.) Limpr. var. *ambigua* (B. S. G.) Craig., *Crossidium chloronotos* (Brid.) Limpr.

— Sur les pierres des ruines de Thuburbo Majus à 58 km au sud-ouest de Tunis (n° 114):

Didymodon rigidulus Hedw. *Tortula intermedia* de Not.

— Sur les ruines d'une piscine romaine au Djebel-Oust (n° 113):

Didymodon rigidulus Hedw., *Barbula revoluta* Brid., *B. unguiculata* Hedw.
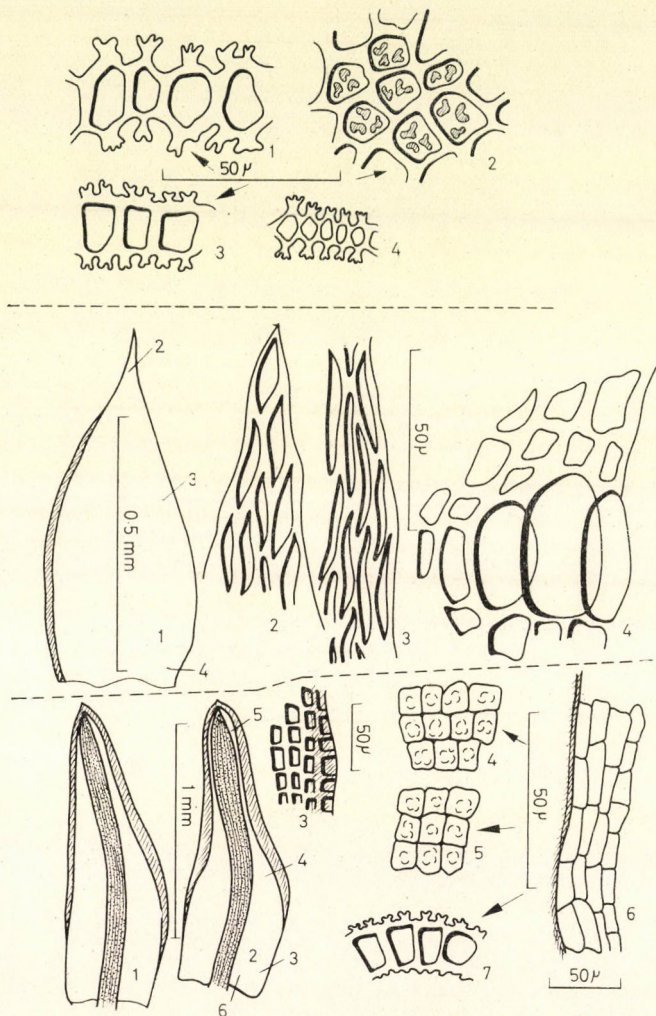
Fig. 3

Tortula ruralis var. *subpapillosissima*:
1, 2: Tissu supérieur de la feuille — 3: *Tortula ruralis*, type
4: *T. papillosissima* Copp. (d'après COPPEY).
Acanthocladium Cuynetii:
1: Feuille — 2, 3, 4: tissu.
Tortula Toutonii:
1,2: Feuilles — 3,4,5,6: Tissu foliaire
7: Coupe au sommet de la feuille.

— Sur les pierres des ruines de Dougga (n° 116):

Didymodon rigidulus Hedw., *Tortula intermedia* de Not.

— Rochers calcaires des pentes méridionales du Djebel Ressas (n° 112 et 118):

Archidium alternifolium (Hedw.) Mitt., *Astomum crispum* (Hedw.) Hamp., *Hymenostomum tortile* (Schwaegr.) B. S. G., *Tortella inflexa* (Bruch.) Broth., *T. media* (Lindb.) Broth., *Didymodon rigidulus* Hedw., *Barbula ungiculata* Hedw., *Phascum curvicolle* Hedw., *Pottia mutica* Vent., *Pottia starkeana* (Hedw.) C. Müll. var. *brachyoda* (B. S. G.) C. Mull., *Aloina rigida* (Hedw.) Limpr. var. *ambigua* (B. S. G.) Craig., *Tortula intermedia* de Not., *Grimmia pulvinata* (Hedw.) Sm., *Ephemerum recurvifolium* (Dicks.) Boul., *Bryum bicolor* Dicks., *B. rubens* Mitt.

Lybie: — Sur les pierres des ruines de Leptis-Magna (N° 123):

Anisothecium varium (Hedw.) Mitt., *Didymodon tophaceus* (Brid.) Garov., *Didymodon rigidulus* Hedw., *Aloinarigida* (Hedw.) Limpr. var. *ambigua* (B. S. G.) Graig.

Dans les listes des espèces recueillies en Afrique de Nord, il faut remarquer la présence de deux espèces particulièrement étudiées par CRUNDWELL et NYHOLM [13] *Bryum radiculosum* et *rubens*. Ces espèces font partie du groupe du *Bryum erythrocarpum* et non de celui de *B. atrovirens* comme l'indique l'Index [25].

Une variété nouvelle **Tortula ruralis** var. n. **subpapillosissima.** Sous ce nom nous désignons une plante intermédiaire entre la forme typique et la var. *papillosissima* qui confirme ce que nous avons écrit sur ce taxon (2.3.). *Tortula papillosissima* décrit par COPPEY comme ayant des cellules portant un bouquet de papilles aigües au sommet d'une colonne d'abord creuse qui se remplit peu à peu [16] et à la fin forme une papille massive. Chez notre variété la cellule est hautement mamilleuse et forme un support surélevé aux papilles en fer à cheval normales chez *T. ruralis* [1] mais cette mamille reste toujours creuse. »A *Tortula papillosissima* (Coppey) Broth. differt papillis cellulosis sejunctis nunquam candellabra formata»[1].

Afrique tropicale

Tchad: — Sur des rochers gréseux près de Bebo au sud de Lai (n° 82):

Fissidens semiobscurus (C. Mull.) Par., *Mönkemeyera flexipes* P. de la Varde, *Hyophila crenulata* C. Mull.

C'est probablement la station la plus septentrionale de ces deux Fissidentacées, *Fissidens semiobscurus* est une espèce de l'Afrique centrale tandis que le *Mönkemeyera* est de République Centrafricaine.

Republique Centrafricaine: — Sur les arbres de la savanne forestière près de Yaloké (n° 84):

Rhacopilum orthocarpioides Broth., *Trachyphyllum pinnatum* (Broth. et Par.) Broth., *Erythrodontium Barteri* (Mitt.) Broth., *Stereophyllum nitens* Mitt.

[1] Toutes ces espèces et variétés nouvelles ont été dessinées par M. R. B. PIERROT. Les échantillons typiques se trouvent dans l'herbier de l'Université de Dijon, les isotypes à Eger.

Conformément au CODE [12] article 73a, contrairement à l'Index nous croyons devoir traduire le ϱ grec par Rh et non R comme le voulait *Bridel*, *Racopilum* et *Racomitrium* doivent donc s'écrire *Rhacopilum* et *Rhacomitrium*.

— Sur la terre d'un talus près de Yaloké (n° 85):

Fissidens ulna (C. Mull.) Par., *F. subdurus* Broth. et P. de la Varde, *Splachnobryum subjulaceum* Card. var. *laxifolium* P. de la Varde, *Brachymenium maclaudi* (Broth. et Par.) P. de la Varde, *Bryum coronatum* Schwaegr.

Plusieurs espèces méritent quelques explications:

Fissidens Ulna est sans aucun doute synonyme de *F. arenivagus* P. de la Varde.

Stereophyllum nitens est identique à une série de formes se séparant par l'acumen de la feuille plus ou moins arrondi, comme *St. contermineum* Card., *St. linguaefolium* (Welw. et Dub.) Gepp., *St. combaniense* Besch., *St. laetevirens* Broth. De l'avis même de CARDOT [21] et d'après les notes de l'herbier THÉRIOT et POTIER DE LA VARDE, il n'existe aucun caractère différentiel, seule l'origine géographique est différente. THÉRIOT concluait: «Toutes ces espèces ne sont que des états d'une seule et meme espèce». Ils est certain que cette liste est incomplète et que d'autres espèces du même groupe doivent y figurer.

Stereophyllum radiculosum. Cette espèce est inséparable de *St. indicum* (Bel.) Mitt déjà connue en Guinée (4.6). Comme pour *St. nitens* la liste des synonymes est grande en Afrique il est probable qu'une bonne partie des espèces du sous genre *Glossophyllum* ne sont que des formes stationnelles de *St. radiculosum*.

En Amérique, GROUT [18], STEERE [14] ont fait la même constatation et donné de nombreux synonymes à *St. radiculosum*.

Gabon: — Sur les arbres à Libreville (n° 69—70):

Octoblepharum albidum Hedw., *Calymperes Palisotii* Schwaegr., *C. subdecolorans* Card., *C. Perrottetii* Besch., *C. intralimbatum* C. Müll., *Thuidium gratum* (P. de Beauv.) Jaeg., *Trichosteleum chrysophyllum* P. de la Varde, *Isopterygium conangium* (C. Müll.) Broth., *Vesicularia latiramea* Broth., *Rhacopilopsis trinitensis* (C. Müll.) Britt. et Dix. var. *acuminata* Card.

— Sur la terre à Libreville (n° 71):

Hyophila crenulata C. Müll., *Semibarbula lambarenensis* (P. de la Varde) Biz., *Bryum ocobiense* Broth. et P. de la Varde.,

— Sur les arbres à Owendo près de Libreville (n° 72):

Fissidens subarboreus Broth. et P. de la Varde., *Syrrhopodon armatus* Mitt., *Calymperes Palisotii* Schwaegr., *C. Perrotteti* Besch., *C. intralimbatum* C. Müll., *Thuidium gratum* (P. de Beauv.) Jaeg.

Calymperes subdecolorans, bien caractérisé par l'absence de stereides dans sa nervure, ne possède pas de feuilles proboscidiennes comme les autres espèces de ce genre. Les propagules sont seulement groupés au sommet de la feuille, comme chez les *Thyridium*, sans que celle-ci s'allonge en trompe d'éléphant.

L'espèce la plus remarquable est *F. subarboreus*, car elle est bien fructifiée et dans ses capsules encore operculées nous avons pu constater que le péristome est formé de 16 dents à peine divisées au sommet. Sur les 15 articles que comporte la dent 5 au plus soit 1/3 sont divisés en 2 branches et ceci sur 1 ou 2 dents seulement sur les 16 que comporte le péristome. Les autres sont entières et irrégulières comme si l'extrémité de la dent était dégénérée. La dent est trabiculée papilleuse jaune orangée, l'extrémité est faiblement papilleuse et à peu près hyaline. Nous avons déjà constaté la même chose sur des échantillons de la Corniche de Bangui, leg. ASSEL (no 761—763). Sur le type de Boukoko de POTIER DE LA VARDE les capsules sout plus âgées et la partie hyaline détruite ce qui rend les dents très entières.

Cette structure insolite montre combien le sporophyte est peu caractéristique chez les Fissidentacées et la fragilité des genres *Monkemeyera*, *Fissidentella* basés sur ce seul caractère.

Cameroun: — Les récoltes du Dr. BALÁZS dans ce pays sont beaucoup plus copieuses, une bonne partie des échantillons provient du Mt. Cameroun.

— Mt. Cameroun pentes méridionales en forêt dense 1400 m (n° 75):

Campylopus Mathieui Thér., *C. viridatulus* C. Müll., *Trachypodopsis serrulata* (P. de Beauv.) Fleisch., *Orthostichidium cameruniae* Dus., *Pilotrichella Mullerii* Dus., *Floribundaria cameruniae* (Dus.) C. Müll., *Calyptothecium longiusculum* (C. Müll.) Broth., *Porothamnium Hildebrandtii* (C. M.) Fleisch., *Daltonia angustifolia* Doz. et Molk., *Hookeriopsis Balazsii* Biz., *Lepidopilum Dusenii* C. Müll., *Actinodontium Dusenii* Broth., *Cyclodictyon vallis-gratiae* (Hampe) O. Kuntze fo. *Breutelianum* (Hampe) Dem. et P. de la Varde., *Thuidium borbonicum* Besch., *T. pycnangiellum* C. Müll., *Rhizofabronia Persoonii* (Schwaegr.) Fleisch. var. *sphaerocarpa* (Dus.) Biz., *Oxyrrhynchium Swartzii* (Turn.) Warnst., *Rhaphidorrhynchium nigricaule* (Brid.) Broth., *Acroporium Pocsii* Biz., *Glossadelphus truncatus* (Welw. et Dub.) Fleisch., *Vesicularia ischyropteris* (Broth.) C. Müll., *Mittenothamnium fruticellum* (Mitt.) Card., *M. frondosum* (Mitt.) Card.

Hookeriopsis Balazsii n. sp.

Planta tota rubro-purpurea, caespites laxi-caulis, folia ovato lanceolata marginibus a medio usque ad summum dentatis, dentibus duobus raro uno aculeatis, nervis binis rubris; Cellulae mediae lineales $5-7 \times 80-100$ μ una minutissima papilla apiculi instructa, basilares hexagono-rectangulae laeves $10-15 \times 60-80$ μ; seta purporeo nigra brevis, caetera desunt.

Cette espèce rappelle *H. papillosula* Broth. et P. de la Varde mais en diffère par sa couleur intense, ses dents géminées, ses cellules allongées vermiculaires finement papilleuses par saillie apicale vers le sommet de la feuille qui est plus longuement acuminée.

Acroporium Pocsii n. sp.:

Folia e basi minuta contractula oblonga subplana raptim in acumen longiusculum fasciaeforme protracta.

Cette espèce rentre dans le cycle de *A. megasporum* (Dub.) Fleisch. mais s'en distingue par sa feuille à peine contractée à la base, plane terminée par un long acumen loriforme, large, rubanné, entier qui rappelle celui de *Rhaphidostichum Schwaneckeanum* (C. Müll.) Broth. d'Amérique du Sud, il est terminée
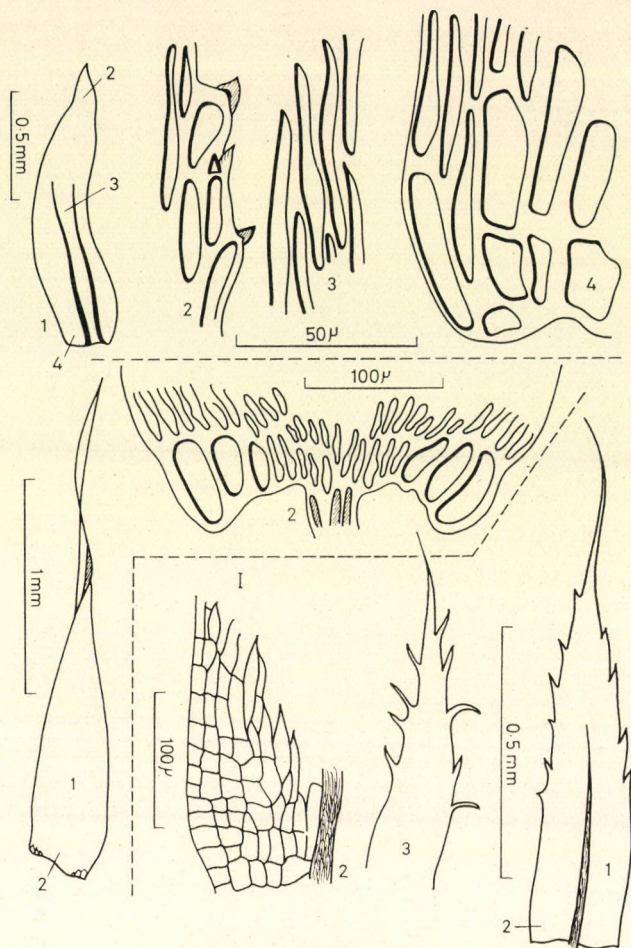
Fig. 4
Hookeriopsis Balazsii: 1—4: Feuille et tissu. *Acroporium Pocsii:* 1, 2: Feuille et tissu.

par une seule cellule allongée 7—10/1 aigüe. La plante est polyoïque le pédicelle ne présente que de rares pustules peu saillantes le péristome est conforme.

Rhizofabronia Persoonii (Schwaegr.) Fleisch. var. **sphaerocarpa** (Dus.) Biz. comb nova, K. Svensk. Vet. Ak. Handl. 28 2:53a, 2 f. 10.1895; *Rhizofabronia spaerocarpa* (Dus.) Fleisch. Musci Fl. Buitenzorg 4:1718. 1923.

Cette variété en représente la forme des régions ombragées et humides le type habite les régions ensoleillées. M. le Dr. Pocs a en effet constaté en Tanzanie où ces deux plantes sont communes tous les intermédaires possibles entre ces deux taxons suivant l'insolation. Nous avons choisi *R. Persoonii* comme type car c'est l'espèce la plus ancienne.

Thuidium borbonicum. Nous rapportons à cette espèce divers échantillons de cette région qui diffèrent de *T. pycnangiellum* par les feuilles périchétiales non ciliées et le pédicelle lisse sauf au sommet où il présente quelques papilles.

— Mt. Cameroun, pentes méridionales en forêt dense 1700 m (n° 76):

Campylopus polytrichoides de Not., *Leptodontium Joannis-meyeri* C. Müll. var. *cameruniae* Broth., *Mnium rostratum* Schrad., *Rhacopilum africanum* Mitt., *Macromitrium levatum* Mitt., *Trachypodopsis serrulata* (P. de Beauv.) Fleisch., *Renauldia Duseni* (Broth.) Broth., *Pilotrichella Muellerii* Dus., *P. gracilicaulis* C. Müll., *Calyptothecium longiusculum* (C. Müll.) Broth., *Hypopterygium viridissimum* C. Müll., *Thuidium borbonicum* Besch. *T. laevipes* Mitt., *Oxyrrhynchium Swartzii* (Turn.) Warnst., *Rhychostegium tenuivagum* (Broth.) Par., *Entodontella cameruniae* Broth., *Acanthocladium Jungneri* Broth., *Glossadelphus truncatus* (Welw. et Dub.) Fleisch., *Sematophyllum brachytheciiforme* (Broth.) Broth., *Acroporium megasporum* (Dub.) Fleisch., *Vesicularia ischyropteris* (Broth.) C. Müll., *Mittenothamnium fruticellum* (Mitt.) Card., *M. frondosum* (Mitt.) Card.

Oxyrrhynchium Swartzii — comme le précédent l'échantillon est stérile la détermination est un peu douteuse mais le gamétophyte ne diffère pas de, la plante européenne.

— Mt. Cameroun, sur le tronc d'une fougère arborescente du genre Cyathea (1800 m) (n° 75):

Rhizofabronia Persoonii (Schwaegr.) Fleisch. var. *sphaerocarpa* (Dus.) Biz.

— Mt. Camerou n pentes méridionales près du chalet refuge n° 1 1900 m (n° 77):

Oxystegus cylindricus (Brid.) Hilps? *Mnium rostratum* Schrad., *Rhacopilum capense* C. Müll., *Renauldia Dusenii* (Broth.) Broth., *Trachypodopsis serrulata* (P. de Beauv.) Fleisch.-*Daltonia angustifolia* Doz. et Molk., *Thuidium laevipes* Mitt., *Brachythecium vellereum* (Mitt., Jaeg., *Rhynchostegium tenuivagum* (Broth.) Par., *Acanthocladium Jungneri* Broth., *Sema*) *tophyllum obtusifolium* (Ren. et Card.) Broth., *Trichosteleum perhamosum* Broth., *Mittenothamnium fruticellum* (Mitt.) Card., *M. frondosum* (Mitt.) Card.

— Mt. Cameroun, sur les arbres et la terre (T) vers 2000 m (n° 60):

Fissidens asplenioides Hedw., *F. purpureocaulis* C. Müll., *F. Darntyi* Besch., *Leucobryum molliculum* Broth., *Leucoloma secundifolium* Mitt., (T) *Funnaria calvescens* Schwaegr., (T) *Rhodobryum Staudtii* (Broth.) Par., (T) *Philonotis hastata* (Dub.) Wijk. et Marg., *Macromitrium levatum* Mitt., *Trachypodopsis serrulata* (P. de Beauv.) Fleisch., *Orthostichidium cameruniae* Dus., *Pilotrichella Muellerii* Dus., *P. gracilicaulis* C. Müll., *Porothamnium molliculum* (C. Müll.) Fleisch., *P. Hildebrandtii* (C. Müll.) Fleisch., *Daltonia angustifolia* Doz. et Molk., *Callicostella perpapillata* Broth. et P. de la Varde., *Lepidopilum Dusenii* C. Müll., *Hypopterygium viridissimum* C. Müll., *Rhynchostegium tenuivagum* (Broth.) Par., *Acanthocladium Jungnerii* Broth., *A. Cuynetii* Biz., *Trichosteleum perhamosum* Broth., *Ectropothecium afromolluscum* Broth., *Trachythecium Le-Testui* Thér. et P. de la Varde., *Vesicularia galerulata* (Dub.) Broth., *Rhacopilopsis trinitensis* (C. Müll) Britt. et Dix.

Fissidens asplenioides que nous citons ici n'est pas distinct de *F. nematopteris* C. Müll. du Cameroun, cette espèce américaine est déjà connue à Madère, elle est identique à *F. Ruwenzorensis* Thér. et Nav. du Congo (Ruwenzori) et *F. Bovinianus* Besch. de la Réunion et de Madagascar. Cette espèce se reconnait facilement à sa lame vraie ouverte s'attachant à la nervure par une courbe, sa lame dorsale étroite décurrente et sa nervure évanescente. C'est une espèce cosmopolite comme *Stereophyllum radiculosum*.

Macromitrium levatum, outre les synonymes donnés par DIXON [15] il faut ajouter *M. tortifolium* Thér. de la Côte d'Ivoire dont le type nous parait identique à *M. levatum*.

Acanthocladium Cuynetii, n. sp.

Cette espèce nouvelle, que nous sommes heureux de dédier à notre ami bryologue averti CUYNET décédé en 1968. Elle est assez proche de *A. Jungneri*, dont elle est une réduction de toutes les parties en particulier du tissu dont les cellules sont très courtes 4—5×50 μ au lieu de 3—4×70—80 μ pour l'espèce de BROTHERUS. Elle diffère des espèces malgaches par ses feuilles entières ou subentières.

«A *Acanthocladio Jungneri* Broth. proxima differt statura minore foliis caulinis minoribus, brevibus acuminatis vel obtusis integerrimis, ramis minute denticulatis; cellulis brevibus 4—5×50 μ».

Nous sommes tout à fait de l'avis de POTIER DE LA VARDE [19] pour séparer *Porothamnium Hildebrandtii* de *Porotrichum comorense* contrairement à l'avis de SIM. [22].

— Mt. Cameroun pentes méridionales à la limite des forêts 2000 m (n° 78):

Campylopus polytrichoides de Not., *C. Bequaertii* Thér. et Nav., *Funaria calvescens* Schwaegr., *Anomobryum juliforme* Solms., *Thuidium borbonicum* Besch., *T. laevipes* Mitt., *Entodon geminidens* (Besch.) Par. ? stérile, *Rhaphidorhynchium nigricaule* (Brid.) Broth., *Acroporium megasporum* (Dub.) Fleisch., *Vesicularia glaucula* (Broth.) Broth., *V. ischyropteris* (Broth.) C. Müll.

— Mt. Cameroun vers le sommet dans une grotte volcanique 2900 m (n° 79):

Fissidens longipes Welw. et Dub., *Campylopus denticuspes* Broth., *Anaectangium euchloron* (Schwaegr.) Mitt., *Oxystegus cylindricus* (Brid.) Help. ? *Fabronia Pocsii* Biz. var. *cameruniae* Biz., *Entodontella cameruniae* Broth.

Fabronia Pocsii n. sp.:

Autoica; caulis irregulariter fastigiatus, ramis rigidis dense foliosis 1—4 mm longis. Folia erecto patentia anguste lanceolata sensim acuminata in cuspidem filiformem elongatam flexuosam marginibus ciliato dentatis. Costa ad vel supra medium continua. Cellulis elongatis prosenchymatosis 7—9×70—120 μ basilaribus quadratis numerosis 9—10 μ. Folia perichaetialia ovato breviter acuminata dentata nec ciliata. Theca vetusa in pedicello 4—5 mm pallido ovatocylindrica erecta 1 mm longa 0,5 mm lata — caetera desunt. (Type Ethiopie.)

var. **cameruniae** n. var.:

A typo differt caulibus laxe foliosis flexuosis angustioribus, longissime ciliatis. (Type Cameroun.)

Cette espèce ressemble étrangement à un *Rhizofabronia* par ses feuilles étroites ciliées son tissu allongé, mais la présence d'une nervure et des cellules basilaires carrées l'en sépare immédiatement.

Elle présente une curieuse convergence avec *Rhizofabronia Persoonii*, comme elle, il existe 2 formes, l'une typique à cils courts, habitant les zones plus sèches (Ethiopie Addis Abeba — Debré — Zeit sur un tronc n° 111) et l'autre, dans la grotte du Mt. Cameroun, avec ses longs cils, parallèles à la variété *sphaerocarpa*.
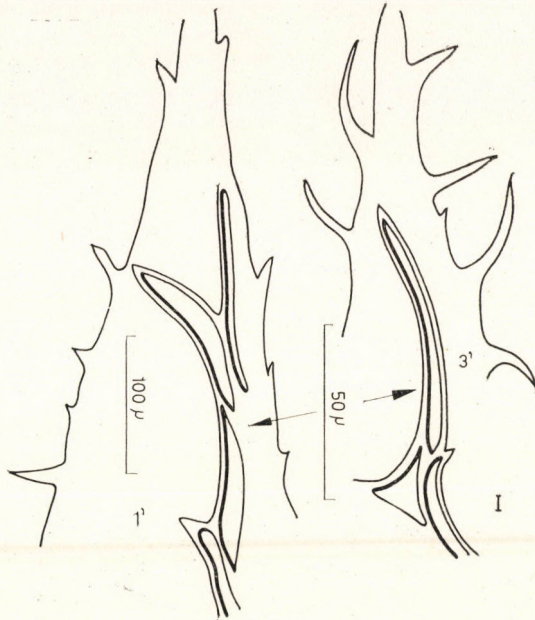
Fig. 5

Fabronia Pocsii:
1, 2: Feuille et tissu, 1' partie moyenne et dent de la feuille. 3: var. *Cameruniae*, feuille partie supérieure, 3' partie moyenne et dent de la feuille.

Cette *Fabronia* est insolite en Afrique, par ses très longs cils foliaires jusqu'à 140 μ atteignant presque la largeur du limbe, elle rentre dans le groupe Bb ε de BROTHERUS.

Elle est très distincte de toutes les espèces africaines par la forme de ses feuilles, son tissu et ses très longs cils. C'est è *F. macroblepharis* Schwaegr. du Brésil que notre espèce ressemble le plus par la forme de la feuille et les cils marginaux mais SCHWAEGRICHEN [23] écrit: «*Fabronia* foliis ovato acuminatis patulo ciliatis enervibus» et le type de POHL (Brésil) correspond bien à cette description. La feuille est pratiquement dépourvue de nervure et ne possède que quelques cellules carrées à sa base 3 à 5 de chaque côté, *F. Pocsii* en a de 15 à 20, et une nervure très nette, en outre le tissu est différent. Notre espèce fait la transition entre les genres *Fabronia* et *Rhizofabronia.*

Fissidens longipes et *Anaectangium euchloron* sont connus aux îles du CAP VERT [8].

— Mt Cameroun vers le sommet sur les rochers volcaniques 3000 m (n° 80):

Campylopus denticuspes Broth., *Leptodontium Joannis* Meyeri C. Müll. var. *cameruniae* Broth., *L. tenerascens* Broth., *Pohlia cratericola* Broth., *Bartramia stricta* Brid., *Polytrichum subformosum* Besch., — Mt Cameroun sur un tronc pourri 3100 m (n° 94): *Leucobryum came-*

runiae C. Müll., — Mt Cameroun au sommet 4000 m (n° 81): *Ceratodon purpureus* (Hedw.) Brid., *Campylopus denticuspes* Broth. var. *acutifolius* Broth., *Leptodontium Joannis* Meyeri C. Müll. var. *cameruniae* Broth., *Grimmia abyssinica* (C. Müll.) Jaegr., *Rhacomitrium alare* (Broth.) Par., *Bryum argenteum* Hedw., *Bartramia Jungneri* Par., *Breutelia subgnaphalea* (C. Müll.) Par., *Hedwigidium integrifolium* (P. de Beauv.) Dix., *Pogonatum afrournigerum* Biz., *Brachythecium Preusii* (Broth.) Par.

— Mt Cameroun vers le sommet sur les roches au bord d'une fumerolle, à la température de 80°, 4000 m (n° 82):

Campylopus polytrichoides de Not. *C. denticuspes* Broth., *Breutelia subgnaphalea* (C. Müll.) Par., *Pogonatum afrournigerum* Biz.

Pogonatum afrournigerum n. sp.:

Sterilis a *Pogonatum urnigero* (Hedw.) P. de Beauv. differt foliis latioribus, minu dentatis, obtusiusculus cellulis basilaribus brevioribus.

S'agit-il d'une bonne espèce? Les petits caractères dont elle diffère suffisent-ils à les séparer des espèces européennes?

Polytrichum subformosum, espèce malgache, très proche de *P. commune* qui s'en sépare par la forme du sillon de la cellule supérieure des lamelles en coupe transversale. Chez *P. commune* le sillon est arrondi en U tandis que chez *P. subformosum* il est aigu en V en plus cette dernière espèce porte au sommet de la feuille des petites dents ou des papilles entre les dents normales de la feuille. Non encore signalé au Cameroun.

— Sur les arbres d'une forêt dense au bord du lac Barombi Mbo, Cameroun occidental (n° 73):

Hypophila crenulata C. Müll., *Groutiella laxotorquata* (Besch.) Wijk. et Marg., *Rhacopilum africanum* Mitt., *Orthostichidium cameruniae* Dus., *Floribundaria jumbeana* (Dus.) C. Müll., *Pilotrichella sordidoviridis* C. Müll., *Pinnatella oblogifrondea* (Broth.) Broth., *P. flagellacea* (Mitt.) Broth., *Porotrichum comorense* Hampe., *Thuidium involvens* (Hedw.) Mitt. var. *thomeanum* Broth., *T. gratum* (P. de Beauv.) Jaeg., *T. laevipes* Mitt., *Fabronia crassiretis* Ren. et Card. *Erythodontium Barteri* (Mitt.) Broth., *Stereophyllum nitens* Mitt., *Acroporium megasporum* (Dub.) Fleisch., *Vesicularia ischyropteris* (Broth.) C. Müll., *Ectropothecium afromolluscum* Broth., *Rhacopilopsis trinitensis* (C. Müll.) Broth. et Dix.

Groutiella laxotorquata. Nous avons déjà parlé de cette espèce (4.7) pour le considérer comme un synonyme de *G. sarcotrichia* (Broth.) Wijk. et Marg.

Fabronia crassiretis espèce de Madagascar bien caractérisée par ses feuilles assez allongées à cellules ovales à paroi épaisse nouvelle pour le Cameroun.

— Sur les arbres près de Doula et à terre (T):

Fissidens diaphanus Biz. nom. mut., *Calymperes leucocoleos* C. Müll., *Octoblepharum albidum* Hedw., (T) *Hyophila crenulata* C. Müll., (T) *Semibarbula lambarenensis* (P. de la Varde) Biz., (T) *Bryum coronatum* Schwaegr., *Cyclodictyon Krebedjense* Broth., *Sematophyllum obtusifolium* (Ren. et Card.) Broth.
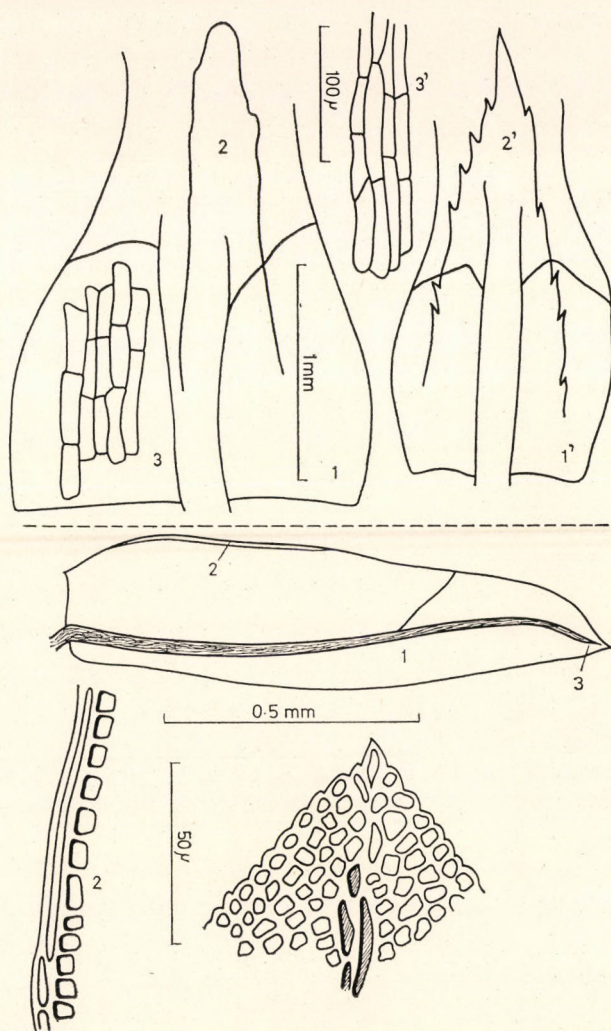
Fig. 6

Pogonatum afrournigerum:
1: base de la feuille — 2: pointe — 3: tissu médian de la graine 1', 2', 3': idem Pog. urnigerum
Fissidens Cuynetii:
1—3: Feuille moyenne et tissu.

Fissidens diaphanus Biz. nom. nov.

Nous avons déjà distingué cette espèce voisine de *F. Marthae* Card. que Potier de la Varde avait nommé *F. leucocaulis* C. M. var. *fallaciosus* [20] mais ce taxon est un nomen nudum. Nous avons élevé cette variété au rang d'espèce comme *F. fallaciosus* (P. de la Varde) Biz. [5] avec une courte dia-

gnose pour valider ce taxon. Malheureusement l'adjectif *fallaciosus* est déjà utilisé par Thériot en 1910 pour un *Fissidens* d'Océanie, notre binôme est donc invalide puisque antidaté par Thériot. Nous le changerons en *Fissidens diaphanus* Biz. nom. nov. qui évoque le tissu presque lisse et translucide de cette espèce.

Semibarbula lambarenensis est nouveau pour le Cameroun.

— Sur les arbres de la cascade Nachtigal du fleuve Sanaga 600 m (n° 89):

Calymperes subdecolorans Card., *C. Quintasii* Broth., *Rhacopilum orthocarpioides* Broth., *Neckeropsis liliana* (Ren.) Par., *Pinnatella oblongifrondea* (Broth.), *Thuidium gratum* (P. de B.) Jaeg., *Stereophyllum radiculosum* (Hook.) Mitt., *S. nitens* Mitt., *Taxithelium subrotundatulum* Broth. et Par., *Vesicularia ischyropteris* (Broth.) C. Müll.

— Sur la terre argileuse près de Ndokayo 900 m (n° 90):

Fissidens dendeliensis Par. et Broth., *Splachnobryum subjulaceum* Card. var. *iaxifolium* P. de la Varde, *Brachymenium Maclaudii* (Broth. et Par.) P. de la Varde.

— Sur la terre près de Yaundé 730 m (n° 91):

Rhacopilum capense C. Müll.

— Sur les arbres près de Yaundé 730 m (n° 92):

Calymperes Quintasii Broth., *Bryum capillare* Hedw. ? *Rhacopilum orthocarpioides* Broth., *Schwetschkea fabronioides* (Welv. et Dub.) Broth., *Erythrodontium Barteri* (Mitt.) Broth., *Entodon geminidens* (Besch.) Par.?

Bryum capillare. L'échantillon est stérile comme *Entodon geminidens*, la détermination reste douteuse.

Neckeropsis liliana est identique à *N. Chevalieri* Broth. et Card [10].

Uganda: — Sur les arbres de la forêt de Mafuga, district de Kigezi 2400 m (n° 95):

Tortula Hildebrandtii (C. Müll.) Broth., *Rhacopilum capense* C. Müll., *Pterogonium gracile* (Hedw.) Sm., *Leptodon Beccarri* C. Müll., *Haplocladium angustifolium* (Hamp. et C. Müll.) Broth., *Thuidium laevipes* Mitt., *Fabronia longipila* Broth., *Schwetschkea fabronioides* (Welw. et Dub.) Broth., *Brachythecium afroglareosum* (Broth.) Par., *B. atrotheca* (Dub.) Besch., *Sematophyllum laetevirens* (Broth. et Par.) Broth., *Hypnum cupressiforme* Hewd., *Pogonatum Potieri* Demar. et Leroy.

— Rochers ensoleillés près de Motozho district d'Ankolé (1300 m) (n° 96):

Fissidens Cuynetii Biz., *Microcampylopus nanus* (C. Müll.) Broth., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hamp.

— Kisoro, Travelers Rest. 2000 m (n° 97):

Campylopus polytrichoides de Not., *Tortella humilis* (Hedw.) Jenn., *Tortula Hildebrandii* (C. Müll.) Broth., *Anomobryum juliforme* Salins., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hampe., *Philonotis hastata* (Dub.) Wijk. et Marg., *Rhacopilum capense* C. Müll., *Pseudoleskeopsis claviramea* (C. Müll.) Thér., *Haplocladium angustifolium* (Hampe et C. Müll.) Broth., *Erythrodontium subjulaceum* (C. Müll.) Par., *Sematophyllum laetevirens* (Broth. et Par.) Broth.

Fissidens Cuynetii n. sp.:

Caespites densi; caulis erectus simplex, folia 6—10 jugis siccicate falcato crispata obovato lanceolata, margine crenulato, nervo flexuoso in brevem mucronem subpercurrente vel longe ante apicem evanescente. Lamina vera ad 2/3 longitudinis folii perveniens ad apicem brevem aperta, lamina apicalis subsymetrica lamina dorsalis ad insertionem enata. Limbus infirme nullus deinde una seriatis formatus, denticulatus ante summum laminae verae evanescens vel totus nullus. Cellulae valde papillosae obscurae rotundato quadrate circa 8 μ lata basilares paulo laxiores subrectangulae. Caetera desunt.

Espèce curieuse par la variation de la longueur de la nervure qui s'éteind très avant le sommet, au moins 10 rangs de cellules, ou atteind le sommet; le limbidium qui n'existe qu'au milieu de la lame vraie, et qui peut être absent sur les feuilles du sommet et de la base de la tige ou même sur la totalité des feuilles.

Tanzanie:

Ce chapitre sommaire sera très développé par M. Pócs lorsqu'il donnera les résultats de son long séjour dans cette région. Nous pensons cependant utile d'indiquer les récoltes de M. Balázs.

— Mt. Meru près d'Arusha sur les arbres 1600 m (n° 98):

Rhacopilum africanum Mitt., *Papillaria africana* (C. Müll.) Jaegr., *Pilotrichella cuspidata* Broth., *Thuidium versicolor* (C. Müll.) Broth., *Erythrodontium subjulaceum* (C. Müll.) Par., *Sematophyllum laetevirens* (Broth. et Par.) Broth.

Mt. Mbeya prés de Mbeya (Tanzania svd), à terre 1850 m (n° 99).

Campylopus polytrichoides de Not., *Didymodon rigidulus* Hedw. var. *acutus* Biz., *Philonotis hastata* (Dub.) Wijk. et Marg., *Rhacopilum africanum* Mitt.

Didymodon rigidulus var. **acutus** n. var.:

A forma typica europaea simili differt: statura majore costa crassiore in mucronem brevem excedente.

Cette variété, qui est peut être une bonne espèce, possède de nombreux propagules identiques à ceux de la plante européenne, elle s'en distingue par sa taille plus robuste, son tissu moins serré, sa feuille plus longuement révolutée mucronée par l'excurrence de la nervure qui se termine par un cellule hyaline comme Amann [1] le signale pour *Barbula vinealis*.

— Mt. Mbeya 2400 m (n° 100):

Pilopogon africanus Broth., *Anaectangium euchloron* (Schw.) Mitt., *Timmiella cameruniae* Broth., *Didymodon rigidulus* Hedw. var. *acutus* Biz., *Tortula Pierrotii* Biz., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hamp., *Entodon Piovanoi* Biz. nom. mut., *Mittenothamnium Overlaeti* Thér. et Nav.

Tortula Pierrotii n. sp.:

Dioica? laxe caespitosa, caulis 10 mm altus, simplex, folia sicca flexuosa erecto incurva, madore patentia 1—1,5 longa obovata obtusa, decurrentia, marginibus integris basi subplanis mox usque a summum latere revolutis; costa valida 60—65 μ sub apice finiente, dorso papillo-
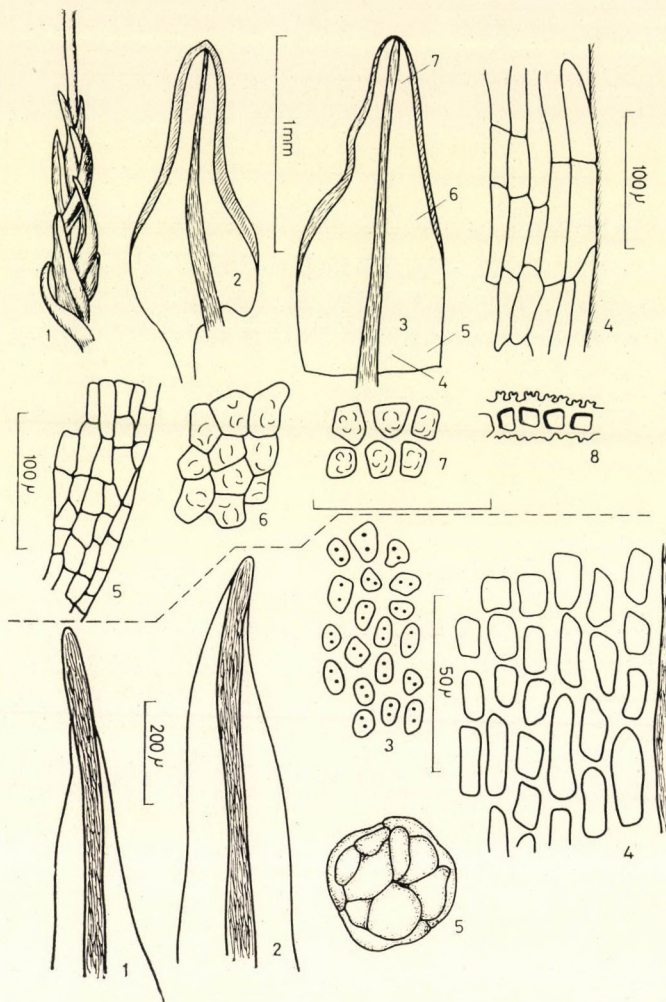
Fig. 7

Tortula Pierrotii:

1: Port à sec — 2, 3: Feuilles — 4, 5, 6, 7: Tissu foliaire — 8: Coupe au sommet de la feuille.

Barbula rigidula var. *acuta:*

1: Pointe de la feuille — 2: *B. rigidula* type — 3: Tissu foliaire médian — 4: Tissu foliaire de la base près de la nervure — 5: propagule.

so; cellulis basilaribus hyalinis juxta costam rectangularibus 10—15×40—50 μ marginalibus subquadratus 10—15×10—15 μ caeteris quadrati rotundatisve subobscuris 12 μ punctatulo papillosis. Perichaetialia similia paulo longiora. Theca juvenis in pedicello pallido 10—12 mm longo cylindrica 2 mm longa pallida operculo longe subulato 1 mm longo. Caetera desunt.

Plante bien curieuse qui rappelle par la révolution de ses feuilles *Barbula revoluta*, également *Tortula atrovirens*, mais la nervure de notre espèce est évanescente et ne porte pas de cellules gonflées fortement papilleuses vers son sommet.

Entodon Piovanoi nom. nov.:

Il s'agit d'une espèce décrite par les R. P. Tosco et Piovano [24] sous le nom de *Entodon abyssinicum* combinaison illégitime car utilisée par Jaeger pour la plante décrite comme Neckera par C. Müller, c'est pourquoi nous la dédions à son auteur le R. P. Piovano, qui nous avait déjà confié d'abondantes récoltes du Brésil [9].

— District de Rungwe, pont naturel près de Lugombo (n° 101):

Campylopus polytrichoides de Not., *Hyophila crenulata* C. Müll., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hamp., *Rhodobryum camptoloma* P. de la Varde, *Philonotis hastata* (Dub.) Wijk. et Marg., *Rhacopilum capense* C. Müll., *Herpetineuron toccoae* (Sull. et Lesq.) Card., *Trachyphyllum fabronioides* (Besch.) Gepp., *Ectropothecium afromolluscum* Broth.

Campylopus polytrichoides est une espèce cosmopolite, cet échantillon possède des lamelles très hautes rappelant la variété alte cristatus Ren. et Card. de Madagascar. Toutes les plantes que nous avons rapporté à *C. polytrichoides* correspondent à la forme définie par Giacomini [17] et non à *C. introflexus.*

— Ngorongoro, côté sud de la Caldera 1600 m (n° 109):

Fissidens longiper Welw. et Dub., *Dicranella usambarica* P. de la Varde, *Acrocryphaea robusta* Broth., *Cryphaea exigua* (C. Müll.) Jaeg., *Leucodon laxifolius* C. Müll. et Fleisch., *Papillaria africana* (C. Müll.) Jaeg., *Pilotrichella cuspidata* Broth., *Neckera subremota* C. Müll., *Porotrichum molliculum* Broth., *Schwetschkea Schweinfurthii* C. Müll., *Palamocladium sericeum* (Jaeg.) C. Müll., *Hypnum cupressiforme* Hedw., *Pogonatum aloides* (Hedw.) P. de Beauv.

Kenya: — Toutes les récoltes ont été faites sur le Mont Kenya:

— Forêt claire sur le flanc occidental 2500 m (n° 102):

Campylopus denticuspis Broth. var. *acutifolius* Broth. *C. procerus* (C. Müll.) Par., *Dicranum acanthoneurum* C. Müll., *Leptodontium Volkensii* Broth., *Tortula Hildebrandtii* (C. Müll.) Broth., *Grimmia ovalis* (Hedw.) Lindb., *Rhacomitrium alare* (Broth.) Par., *Tayloria serrata* (Hedw.) B. S. G. var. *tenuis* (With.) B. S. G., *Breutelia Stuhlmanii* Broth., *Zygodon seriatus* Thér. et Nav., *Z. intermedius* B. S. G., *Macromitrium protractum* Broth., *Antitrichia curtipendula* (Hedw.) Brid., *Pterogonium gracile* (Hedw.) Sm., *Brachythecium atrotheca* (Dub.) Besch., *B. ramicola* Broth., *Sematophyllum subbrachytheciiforme* P. de la Varde, *Hypnum cupressiforme* Hedw.

— Rochers sur le flanc occidental 3000 m (n° 103):

Campylopus denticuspis Broth., *C. bartramiaceus* (C. Müll.) Thér., *Dicranum Johnstonii* Mitt., *Leptodontium Joannis* Meyeri C. Müll., *L. tenerascens* Broth., *Grimmia ovalis* (Hedw.) Lindb., *Rhacomitrium durum* (Broth.) Par., *R. alare* (Broth.) Par., *Hedwigidium integrifolium* (P. de Beauv.) Dix., *Porotrichum comorense* Hampe., *Sematophyllum subbrachytheciiforme* P. de la Varde.

— Turbière sur le flanc occidental 3500 m (n° 104): parmi les *Sphagnum.*

Campylopus stramineus (Mitt.) Jaeg., *Breutelia stricticaulis* Dix.

— Sur les rochers ensoleillés de la Vallée Teleki 3900 m (n° 105):

Ceratodon purpureus (Hedw.) Brid., *Campylopus stramineus* (Mitt.) Jaeg., *Leptodontium Joannis Meyeri* C. Müll., *L.* (?) *Allorgei* Biz., *Grimmia ovalis* (Hedw.) Lindb., *Rhacomitrium alare* (Broth.) Par., *Breutelia subgnaphalea* (C. Müll.) Par., *Hedwigidium integrifolium* (P. de Beauv.) Dix., *Hypnum cupressiforme* Hedw.

— Rochers au bord de la rivière dans la vallée TELEKI 4000 m (n° 106):

Ceratodon purpureus (Hewd.) Brid., *Campylopus stramineus* (Mitt.) Jaeg., *Grimmia ovalis* (Hedw.) Lindb., *Rhacomitrium durum* (Broth.) Par., *Bryum Hedbergii* P. de la Varde, *Orthotrichum* sp.? sterile, *Antitrichia curtipendula* (Hedw.) Brid., *Drepanocladus exannulatus* (B. S. G.) Warnst., *Brachythecium rivulare* B. S. G., *B. vellereum* (Mitt.) Jaeg., *Hypnum cupressiforme* Hedw.

— Rochers près du chalet refuge Klarwills-Hut dans la vallée Teleki 4160 m (n° 107):

Ceratodon purpureus (Hedw.) Brid., *Campylopus stramineus* (Mitt.) Jaeg., *Leptodontium Joannis Meyeri* C. Müll., *L. abyssinicum* Broth., *Tortula Hildebrandtii* (C. Müll.) Broth., *Grimmia ovalis* (Hedw.) Lindb., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hamp., *Orthorichum* sp? sterile, *Hedwigidium integrifolium* (P. de Beauv.) Dix.

— Rochers près du sommet 4800 m (n° 108):

Grimmia ovalis (Hedw.) Lindb.

Leptodontium (?) Allorgei n. sp.:

Caespites dense aggregati inferne nigrescentes superne luteo virides; caulis erectus 3 cm longus simplex vel irregulariter divisus, folia sicca flexuoso crispata, madida erecto flexuosa 1—1,5 mm longa 0,50—0,70 lata e basi ovata sensim angustata lanceolata subobtusa, canaliculata marginibus minus reflexis minute denticulatis costa crassa 70—75 μ sub apicem evanida dorso fere e basi ad summum horride papillosa. Cellulis basilaribus laevibus hyalinis rectangularis 10×60—70 μ ad marginem quadratis caereris quadratis rotundatisve 8—10 μ una majuscula papilla ornatis. Folia perichaetialia vaginante laevis laxe reticulata brevissime acuta costa evanescente. Theca junior in pedicello laevi flavido 12—15 mm cylindrica inclinata 1,5 mm operculo longe subulato 1 mm. Calyptra subulata.

La caractéristique de cette espèce est le tissu dont les cellules portent une unique papille très longue cylindrique, et la nervure très fortement papilleuse. Aucune espèce de ce genre ne présente ces caractères, s'agit-il bien d'un *Leptodontium?* le péristome n'étant pas encore différencié il est difficile de l'affirmer. Il est mélangé (?) avec *L. Joannis Meyeri*. Nous sommes heureux de le dédier à Madame ALLORGE, directrice de la Revue Bryologique et Lichénologique.

La flore du Mont Kenya est un curieux mélange d'espèces temperées et africaines l'altitude en est certainement l'explication qui permet l'existence de plantes comme *Grimmia ovalis*, *Antitrichia curtipendula* (identique à *A. kilimandscharica* Broth.) *Drepanocladus exannulatus*. Nous citons le genre *Orthotrichum* bien que l'échantillon stérile ne puisse être déterminé avec certitude car ce genre nous paraît nouveau pour la région.

Ethiopie: Toutes les récoltes proviennent d'Addis Abeba, Debré Zeit entre 1800 et 2600 m (n° 111):

— Un premier groupe recueilli sur les arbres:

Tortula Hildebrandtii (C. Müll.) Broth., *Bryum torquescens* Bruch., *B. argenteum* (Hedw.) var. *lanatum* (P. de Beauv.) Hamp., *Fabronia Pocsii* Biz., *F. leikipiae* C. Müll., *Entodon Piovanoi* Biz., *Brachythecium populeum* (Hedw.) B. S. G., *Rhynchostegium Jovet-Astii* Biz., *Hypnum cupressiforme* Hedw.
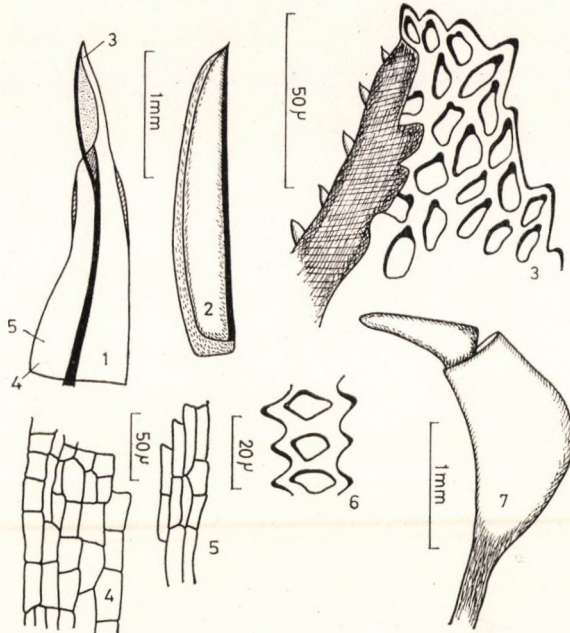
Fig. 8
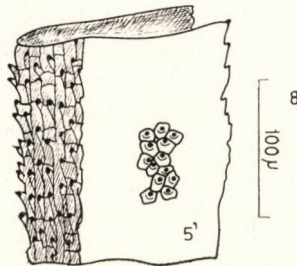
Fig. 9

Leptodontium Allorgei:
1, 3, 4, 5: Feuille moyenne et tissu — 2: F. périchétiale — 6: Coupe de la feuille près du sommet — 7: Capsule avortée — 8: Dos de la nervure.

Rhynchostegium Jovet-Astii n. sp.:

Habitu *Oxyrrhynchii Swartzii* (Turn.) Warnst. similis. Caulis elongatus flacidus robustiuculus. Folia caulina haud decurrentia ovata acuminata denticulata. Theca nigra in pedicello rubro laevi 10 mm longo erecta ovato cylindrica 1,5 mm longa 0,80 lata operculo oblique rostrato 1—1,2 mm longo. Exostomi dentes elongati lanceolato-subulati 0,50 mm endostomium latescens granulosum, processibus in carina haud fissis, ciliis nullis, membrana 85 μ, Annulus simplex. Sporae minutissime granulosae 15—17 μ.

Espèce très curieuse par son sporophyte qui rappelle les genres américains *Eriodon* et *Mandoniella*. Nous le rangeons provisoirement dans les *Rhynchostegium* à cause de son pédicelle lisse bien que la nervure soit épineuse comme *Eurhynchium*.
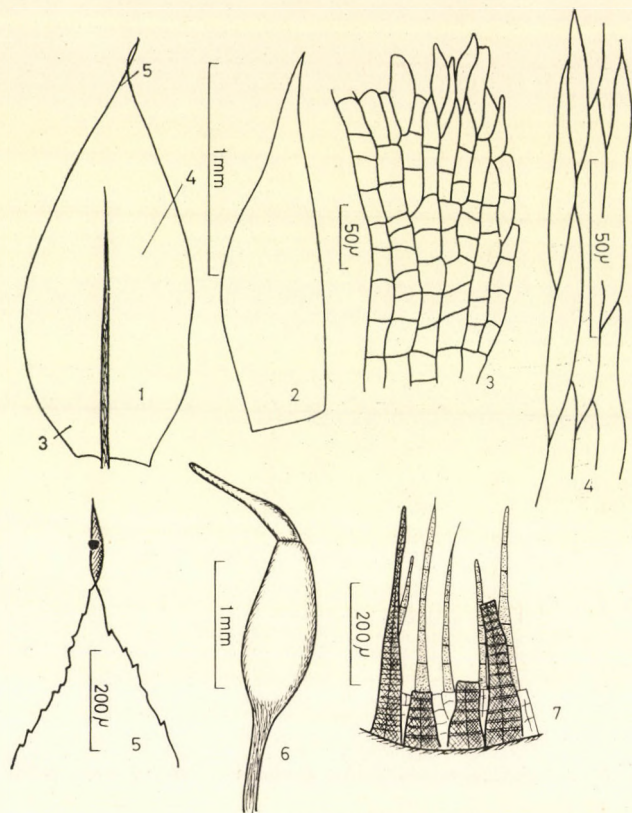
Fig. 10

Rhynchostegium Jovet-Astii:
1, 3, 4, 5: Feuille caulinaire et tissu — 2: F. périchétiale — 6: Capsule — 7: fragment du péristome.

— Le deuxième groupe a été recueilli sur la terre rocheuse d'une forêt d'*Eucalyptus*:

Fissidens longipes Welw. et Dub., *F. pseudoserratus* (C. Müll.) Jaeg. ? *Campylopus brevipilus* B. S. G., *Pleurochaete Beccarii* Vent., *Timmiella barbuloides* (Brid.) Mönk., *Didymodon rigidulus* Hedw., *Tortula Toutonii* Biz., *T. Hildebrandtii* (C. Müll.) Broth., *Anomobryum filiforme* (Dicks.) Solms., *Brachymenium abyssinium* (C. Müll.) Bruch. et Schimp., *Bryum argenteum* Hedw. var. *lanatum* (P. de Beauv.) Hamp., *B. capillare* Hedw., *Bartramia stricta* Brid., *Haplocladium angustifolium* (Hamp. et C. Müll.) Broth., *Thuidium versicolor* (C. Müll.) Broth., *Pseudoleskeopsis claviramea* (C. Müll.) Thér., *Pogonatum oligodus* (C. Müll.) Mitt.

Tortula Toutonii n. sp.

Sterilis caespites densiusculi caulis 5—8 mm altus simplex; folia sicca spiraliter contorta, madida palentia rigida 1 mm longa haud decurrentia obtusa marginibus basi usque ad summum revolutis; costa pervalida 95—100 μ superne paulo dilatata dorso papillosa in apice fissiente vel clavato brevi excedente, cellulis basilaribus luteus ad costam majoribus rectangularibus 12×35—40 μ ad marginem quadratis 14—15 μ caeteris quadratis 10 μ, papillis 4 majusculis semilunatis ornati. Caetera ignota.

Espèce assez voisine de *T. Pierroti* nous pensions à une variété mais la spiralisation extrèmement vive des feuilles à sec, la forme des papilles, la révolution des feuilles suffisent à distinguer les deux plantes. Nous sommes heureux de dédier cette espèce à M. TOUTON en hommage à ses travaux bryologiques.

Conclusion

L'étude de cet abondant matériel nous a permis de reconnaître plusieures espèces et variétés nouvelles:

Acanthocladium Cuynetii, *Acroporium Pocsii*, *Didymodon rigidulus* var. *acutus*, *Fabronia Pocsii*, *Fabronia Pocsii* var. *cameruniae*, *Fissidens Cuynetii*, *Hookeriopsis Balazsii*, *Leptodontium* (?) *Allorgei*, *Pogonatum afrournigerum*, *Rhynchostegium Jovet-Astii*, *Tortula Pierrotii*, *Tortula ruralis* var. *subpapillosissima*, *Tortula Toutonii*.

Elle nous a fait constater la présence d'espèces dont l'origine est parfois éloignée comme *Thuidium borbonicum*; reconnaître l'identité de diverses espèces, comme celle de *Stereophyllum radiculosum* avec *Stereophyllum indicum* ainsi que celle de *Stereophyllum nitens* avec diverses espèces africaines. En outre, M. BALÁZS a eu la chance de récolter *Fissidens subarboreus* bien fructifié et nous avons ainsi confirmé les idées de POTIER DE LA VARDE sur le genre *Moenkemeyera*. Caracterisé par un péristome à dents entières, il est lié par des transitions insensibles au genre *Fissidens* dont les dents péristomiales se divisent en deux branches depuis la moitié.

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NEW PLANTS IN CUBA II.

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The present study (second publication of the authors in this series) involves the descriptions of further 16 new taxa discovered in Cuba by the authors on their expeditions of vegetation mapping. At the same time the paper contains the taxonomic revision of some problematic polymorphic species of the Flora of Cuba, e.g.: *Amyris stromatophylla* P. Wils., and *Tabebuia petrophila* Greenm. as well as the phototypes or photoisotypes of some earlier (in Borhidi, A.—Muñiz, O.: New Plants in Cuba I; Acta Bot. Acad. Sci. Hung. **17**, 1971. 1—36.) taxa.

The new taxa are as follows: **Rutaceae:** *Amyris* (2 ssp.); **Euphorbiaceae:** *Leucocroton* (1 sp.), *Platygyne* (2 sp.); **Buxaceae:** *Buxus* (1 sp., 1 var.); **Celastraceae:** *Gyminda* (1 sp.); **Sapindaceae:** *Thouinia* (1 var.); **Rhamnaceae:** *Rhamnidium* (1 sp.); **Bignoniaceae:** *Tabebuia* (1 ssp.); **Gesneriaceae:** *Rhytidophyllum* (1 sp.); **Rubiaceae:** *Exostema* (1 var.); **Asteraceae:** *Heptanthus* (1 sp.), *Eupatorium* (1 sp.), *Vernonia* (1 var.).

Rutaceae

Amyris stromatophylla P. Wils.

1 a Foliola obtusa, emarginata vel incisa, apice non mucronata, margine integro, pedunculus 2—8 mm longus 2

b Foliola plerumque acuta, apice mucronata, margine denticulato-serrato; inflorescentia laxa, pedunculus 5—15 mm longus (Valle de Yumuri, solo calcareo) .... ssp. **yumuriensis**

2 a Foliola oblongo-obovata vel oblongo-elliptica, 2—3 cm lata; fructus 5—7 mm diam. (Sierra de Nipe; solo lateritico in rupestribus serpentinicis) .... ssp. **stromatophylla**

b Foliola rhomboidea vel late elliptica, 3—5.5 cm lata; fructus globosus, 8—10 mm diam. (Sierra de Moa; solo lateritico in rupestribus serpentinicis) .... ssp. **moaënsis**

ssp. yumuriensis Borhidi et Muñiz ssp. nova

A typo differt: foliolis apice acuminatis vel acutis, mucronatis, margine serrulato-denticulato, inflorescentia laxiore, pedunculo 5—15 mm longo et 0.5 mm in diam., pedicellis 2—5 mm longis, 0.2—0.3 mm crassis.

Typus: Prov. Oriente: Valle de Rio Yumuri inter Baracoa et Maisi; leg.: Hno León 17400 LS.

ssp. **moaënsis** Borhidi et Muñiz ssp. nova

A typo differt: foliolis rhombeis vel late ellipticis, ovatis vel obovatis, apice profunde incisis, 6—9 cm longis, 3—5.5 cm latis, inflorescentia terminalis, densa, breviter corymbosa, pedunculo 3—4 mm longo et 0.8—1.0 mm in diam., pedicellis 1—3 mm longis, fructibus 8—10 mm diam.

Typus: Prov. Oriente: Moa: Mina Delta; leg. J. Acuña 12453 SV. — Moa: Mina Cayoguan; leg. Hno Alain, Clemente et Crisogono, Al. 882. LS.

Euphorbiaceae

Leucocroton moaënsis Borhidi et Muñiz sp. nova (Fig. 1)

Frutex vel arbor parva dioica, 4—5 m alta. Rami vetustiores glabri, cortice grisacei, striati, hornotini squamulis inaequaliter et radiatim ramulosis albidis floccoso-tomentosuli, internodiis variis, 4—20 mm longis. Folia petiolis 6—10 mm longis, supra profunde sulcatis, glabrescentibus, muricato-tuberculatis, anguste oblongo-oblanceolata vel lineari-lanceolata, 5—13 cm longa, 0.8—1.6 cm lata, apice obtusa et mucronulata, basi longe cuneata, nervo medio supra anguste profundeque impresso, subtus valde prominente, lateralibus utroque latere 25—40 pinnatim dispositis sub angulo 80—90° abeuntibus, plerumque rectis, supra obsoletis, subtus valde prominentibus, reticulatis et transversim anastomisantibus, in statu juvenili utrinque dense albo-lanata, demum glabra, supra nitida et in sicco olivaceo-viridia, subtus opaca, pilis multiradiatis albido-tomentosa, adjectis pilis ad nervos venasque paullo longioribus obtecta, postremo glabra, vel inter nervos, pulverulenta margine revoluta coriacea.

Inflorescentiae in apice ramorum ex axillis hypsophyllorum bracteiformium lineari oblanceolatorum, 5—8 mm longorum prodeuntes, masculae tantum visae, pedunculis 0.8—1.5 cm longis, pilis rectis albo-pubescentibus, apice capitatae, 6—10 mm in diametro. Bracteae lanceolatae, obtusae, concavae, usque ad 3 mm longae, crassae; pedicelli nulli. Flores masculi: Alabastra globulosa, albo-tomentosa, usque ad 2 mm diam. Sepala 5, ovata, acuta. Discus tenuis. Stamina 8, margine receptaculi convexi dense albido-pilosi inserta; antherae subquadratae. Ovarii rudimentum nullum. Inflorescentia feminea nobis ignota.

Obs.: E sectione *Asystemon* Urb., *L. Ekmanii* Urb. affinis, quis foliis obovatis, 2—5.5 cm latis, subtus permanente flavido-tomentosis, nervis lateralibus supra tenuiter prominulis et reticulatis, pedunculis 2—4 cm longis, quadrang.ularibus, 1—2 mm crassis, flavido-floccosis, sepalis obtusis bene discrepat

Typus: Prov. Oriente; Region de Moa; in pluviisilvis saxosis serpentinosis montanis reservationis Cupeyal del Norte, supra rivum Rio Toa, 800 m. s. m. Leg. A. Borhidi, O. Muñiz et S. Vazquez, 10. II. 1970. SV sine num.; isotypus: Bp.

Platygyne triandra Borhidi sp. nova

Caulis volubilis fruticosus; folia subcoriacea, breviter petiolata, linearia vel lineari-elliptica, 1.5—3 cm longa, 0.6—1.2 cm lata, apice acuta et mucronato-denticulata, basi rotun data vel subcordata, margine denticulato, supra lucida, sparse ferrugineo-setulosa, demum glabra, subtus pallida et glabrescentia, ad nervos pilis brevibus et patentibus ferrugineis, pi lis urentibus utrinque obsita, nervis utrinque prominentibus.

Flores masculini in inflorescentia spiciformi, densiter bracteosa, 1—2 cm longa, pedicellis brevibus vel nullis; sepala 3—4, late ovata, 1.5—2 mm longa, apice acuta; stamina 3 (4). filamentis brevibus, glabris; receptaculum ferrugineo-pilosum. Flores feminei: sepala 5—6, lanceolata, acuta, 3.5—4.5 mm longa, ferrugineo-pilosa; styli 3, oblongo-lineares, apice emarginati et breviter bifidi; ovarium triloculare, extus albo-setulosum.

Fig. 1. Leucocroton moaënsis Borhidi et Muñiz, isotype specimen, Bp.

Obs.: Habitu, forma foliorum *P. hexandrae* (Jacq.) Muell. Arg. affinis, quae staminibus 5—8, sepalis masculinis lanceolatis, foliis subtus albo-sericeis, stylis apice dilatatis et crenulatis valde differt.

Typus: Borhidi 1721. Prov. Oriente; Sierra de Nipe: in fruticetis sempervirentibus montanis solo lateritico serpentinoso montis Loma Mensura supra Pinares de Mayari 650—950 m. s. m. — Leg. A. Borhidi et O. Muñiz, 18. VII. 1970. Bp; isotypus: SV.

Specimina examinata: LF 1593; Sierra de Nipe: Finca la Caridad, leg. M. LOPEZ FIGUEIRAS. — Alain 4666; Falda Sur de la Sierra de Cristal, leg. HNO ALAIN et M. LOPEZ FIGUEIRAS. — LF 1255; Moa: Cerro de Miraflores de Cananova, leg. M. LOPEZ FIGUEIRAS. — LEÓN 21246; Región de Moa, leg. HNO LEÓN.

Platygyne obovata Borhidi sp. nova (Fig. 2)

Caulis volubilis fruticosus; folia chartacea, usque ad 5 mm longe petiolata, petiolis dense ferrugineo-setulosis, 3—5.5 cm longa, 1—3 cm lata, obovata vel oblongo-obovata, apice rotundata et mucronulato-denticulata, basi obtusa vel rotundata, rariter subcuneata, margine remote mucronulato-denticulata, pilis urticantibus utrinque obsita, supra sparse ferrugineo-setosa, demum glabra, subtus ad nervos ferrugineo-setoso-hirsuta, demum glabrescentia, nervis supra prominulis, subtus valde prominentibus.

Flores masculini fasciculati, pedicellati, sepala 4—6, late ovata, 2—2.5 mm longa, apice acuta, ferrugineo-hirsuta; stamina 5—8, antherae ellipticae, filamenta glabra, receptaculum ferrugineo-pilosum. Flores feminei: sepala 5—6, lanceolata vel lineari-lanceolata, 5—7 mm longa, acuta et acuminata; styli 3—4, oblongo-ovati vel lineari-oblongati, pars libera 3—4 mm longa, apice integri et acuti. Ovarium albo-setulosum, 3 (4)-loculare; ovulum 1.

Obs.: Habitu, forma foliorum *P. Leonis* Alain affinis, quae filamenta pilosa, stamina 8—10, antheris orbicularibus bene differt. *P. volubilis* Howard a planta nostra foliis basi cuneatis subtus pilis urentibus absentibus sepalis femineis 6—9, longioribus et stylis bifidis differt.

Typus: Bp 503529. Prov. Oriente: Region de Moa; in pinetis humidis vallis rivi Rio Toa, in reservatione Cupeyal del Norte, 500 m. s. m. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 9. II. 1970. Isotypus: SV.

Specimina examinata: Bp 503298; Prov. Oriente: Region de Moa, in pluviisilvis saxosis montanis vallis superioris rivi Rio Toa, in reservatione Cupeyal del Norte, 800 m. s. m. Leg. A BORHIDI, O. MUÑIZ et S. VAZQUEZ, 10. II. 1970. — Prov. Oriente: Region de Moa, in pinetis pr. pag. Punta Gorda. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 18. II. 1970. — Prov. Oriente: Region de Moa, in pinetis ad Cayo Chico supra pag. Moa, in 450 m. s. m. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 25. III. 1970. — Prov. Oriente: Region de Baracoa, in fruticetis sempervirentibus serpentinosis ad "El Pino", Peladeros de Jauco inter pag. La Tinta et Baracoa. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 21. III. 1970.

Euphorbia Munizii Borhidi (Fig. 3)

See the description of the species in Acta Bot. Acad. Sci. Hung., **17,** (1971) p. 11.

Euphorbia helenae Urb. ssp. **grandifolia** Borhidi et Muñiz (Fig. 4)

Diagnosis of the subspecies to be found in Acta Bot. Acad. Sci Hung., **17,** (1971) p. 11.

Fig. 2. Type specimen (Bp 503529) of *Platygyne obovata* Borhidi
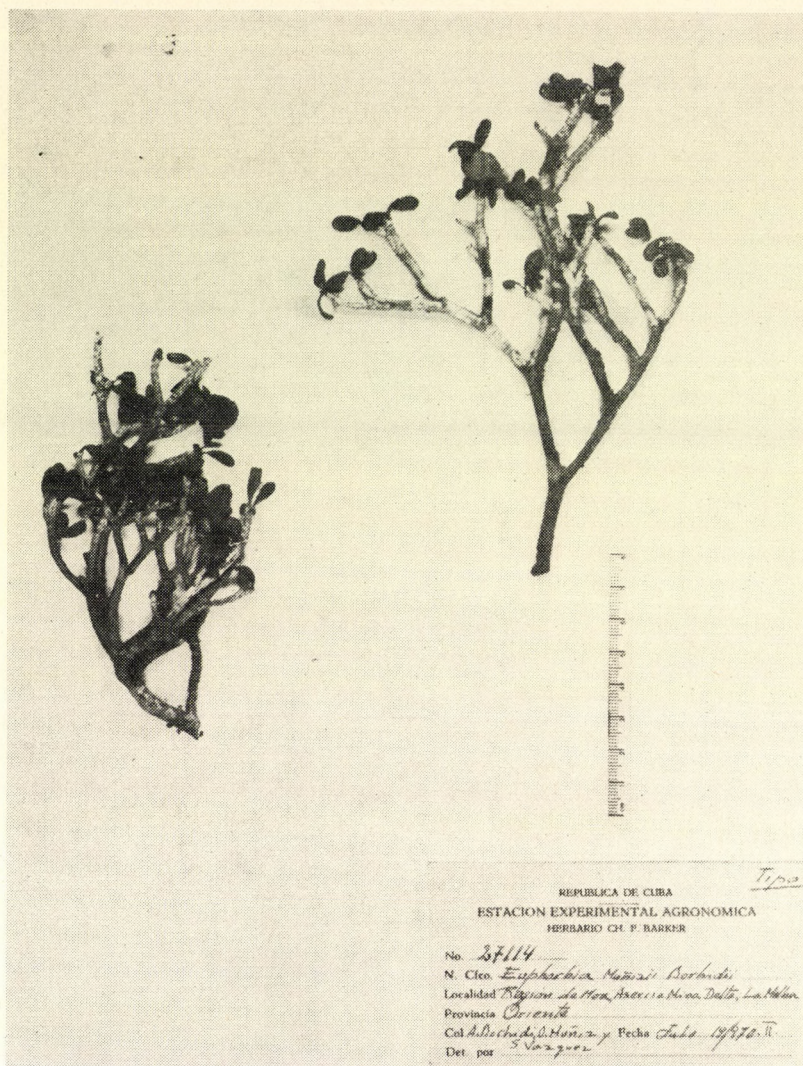
Fig. 3. Type specimen (SV 27114) of *Euphorbia Munizii* Borhidi

Buxaceae

Buxus baracoënsis Borhidi et Muñiz sp. nova

Frutex 2–3 m altus. Rami vetustiores quadrangulares, hornotini anguste 4-alati, glaberrimi; internodiis 1–1.5 cm longis. Folia coriacea, 2–3 mm longe petiolata, petiolis alatis, basi dilatatis, ad nodum proximum decurrentibus, elliptica vel ovato-elliptica, basi breviter angustata et in petiolum contracta, antice rotundata et emarginata, minute mucronulata, 1–1.8 cm longa, 0.5–0.9 cm lata, nervo medio supra impresso, subtus inferne crassiuscule prominente, versus apicem plano vel paullo impresso, nervis lateralibus utrinque inconspicuis,

Fig. 4. Type specimen (SV sine numero) of *Euphorbia helenae* ssp. *grandifolia* Borhidi et Muñiz

supra in sicco flavo-viridia, nitida, subtus pallide glauca, punctulis albis prominulis dense obtecta, margine incrassata, revoluta.

Inflorescentiae axillares, 2—2.5 mm longe pedunculatae, 6—7 mm longae. Bracteae inferiores vacuae, triangulares, acutae, 1 mm longae, flores suffulcientes obtusiusculae, omnes

puberulae et margine dense ciliatae. Flores masculi: pedicelli quadrangulares, 1—2 mm longi; sepala ovato-elliptica, obtusa vel truncata, 1.5—2 mm longa, margine breviter ciliata, filamenta 1.4—1.8 mm longa, superne paullo dilatata, antherae oblongo-ellipticae, 0.6—0.8 mm longae. Ovarium rudimentum ovoideum. Flores feminei: sepala ovata, externa 0.6—0.7, interna 1 mm longa, dense ciliata. Ovarium globosum, minute et dense albido-pilosum, 1—1.5 mm in diametro, stylis 2—3-plo brevius. Styli inter sese liberi, 2.5—3 mm longi, in 3/4—4/5 parte superiore stigmatosi, stigmatibus late linearibus, aequilatis, 0.6 mm latis, intus longitrorsum profunde sulcatis ad apicem recurvis, dimidii intus convexis.

Obs.: *B. Shaferi* (Britt.) Urb. affinis, quae foliis majoribus, 1.5—3.5 cm longis, nervis lateralibus conspicuis, capsula stylis duplo longiore valde discrepat.

Typus: Prov. Oriente: in fruticetis serpentinosis "El Pino" ad Palderos de Jauco, inter opp. Baracoa et pag. La Tinta. Leg. A. Borhidi, O. Muñiz et S. Vazquez, 21. III. 1970. SV sine numero; isotypus: Bp.

Buxus crassifolia (Britt.) Urb.

var. **crassifolia:** foliis elliptico-obovatis, 3—6 cm latis;

var. **oblongata** Borhidi et Muñiz var. nova: foliis oblongo-ellipticis, 1.5—2.5 cm latis. Typus: Clemente 3627; Prov. Oriente: Region de Moa, Rio Yagrumaje. LS.

Celastraceae

Gyminda orbicularis Borhidi et Muñiz sp. nova

Arbor parva, dioica, ramosissima, usque ad 3 m alta; ramuli hornotini quadrangulares, brunnescentes, glabri, vetustiores cortice albicanti glabri adhaerente. Folia opposita vel subopposita usque ad 1 mm longe petiolata, orbicularia vel late orbicularia, 5—10 mm longa et 6—11 mm lata, utrinque glabra, supra in sicco, pallide glaucescentia, subtus pallide punctata, apice emarginata, basi rotundata vel subcordata, margine minute crenulata, incrassata et revoluta, nervo medio utrinque prominulo usque ad dimidium limbi, apicem versus applanato vel evanescente, nervis lateralibus supra nullis, subtus in statu juvenili conspicuis, paullo impressis, 2—3 paribus arcuatis, reticulato anastomisantibus demum obsoletis, coriacea vel subcoriacea.

Inflorescentia mascula tantum visa: cyma 3-(5)-flora, axillaris; pedunculus 4—8 mm longus, quadrangularis, glaber, cyma bibracteata, bracteis ovatis, 0.5—0.7 mm longis; flores laterales 1—1.5 mm longe pedicellati, minores, 4-bracteatis, in alabastro 0.5 mm longi, saepe steriles, sine rudimentum ovarii. Flos centralis sessilis, major, in alabastro 1 mm in diametro, sepala 4, ovata, 0.5—0.7 mm longa, basi connata, margine pilosa; petala 4, orbicularia, 1 mm longa, concava, alba vel rosea, glabra. Discus applanatus, 4-lobulatus, stamina 4, in sinubus disci inserta, filamenta glabra, 0.5 mm longa, antherae globosae vel late ovatae, 0.5 mm longae; rudimentum ovarii in disco connatum, verisimiliter 2-loculare. Styli 2, basi connati, subalati, 0.1—0.2 mm longi. Flores feminei fructusque ignoti.

Obs.: Species generis *Gymindae* Sarg. adhuc monotypici cognati. *G. latifolia* (Sw.) Urb. foliis obovatis, basi cuneatis, multo majoribus, sepalis rotundatis, floribus duplo majoribus optime differt.

Typus: SV 27123; Prov. Oriente: in fruticetis saxosis calcareis aridis supra vallem rivi Rio Jauco pr. pag. Jauco. Leg. A. Borhidi, O. Muñiz et S. Vazquez, 17. III. 1970. Isotypus: Bp.

Sapindaceae

Thouinia elliptica Radlk.

var. **rotundata** Borhidi et Muñiz var. nova

A typo differt foliolis minoribus, late ovatis vel orbicularibus, apice basique rotundatis, margine integro.

Typus: Prov. Oriente: Yunque de Daiquiri, in saxosis calcareis aridis, alt. 50 m. s. m. Leg. A. BORHIDI 29. XI. 1969. SV. sine numero; isotypus: Bp. — Prov. Oriente: Yunque de Daiquiri, leg. M. LOPEZ FIGUEIRAS.

Rhamnaceae

Rhamnidium potrerilloanum Borhidi et Muñiz sp. nova

Frutex 1—2 m altus. Rami vetustiores teretes, striati, sparse lenticellati, $\pm$ glabri, hornotini dense breviterque puberuli, paullo striati, fuscescentes. Stipulae interpetiolares non connatae, anguste oblongo-lanceolatae, apice brevissime bifidae, 3—4 mm longae, dorso 2 nervis prominentibus, in apiculos excurrentibus, margine ciliatae. Folia opposita vel subopposita 3—5 mm longe petiolata, petiolis 4—6 glandulis prominentibus obsitis, puberulis, oblongo-ovata, oblongo-elliptica vel oblongo-obovata, basi breviter cuneata, truncata vel rariter rotundata, antice subsensim angustata, apice ipso acuta vel obtusa, et brevissime mucronata, rariter emarginata, 3.5—6 cm longa, 1.2—2 cm lata, nervo medio supra vix impresso, subtus valde prominente, nervis lateralibus utroque latere 8—11, sub angulo 50—60° abeuntibus, utrinque tenuiter prominentibus et anastomisantibus, minute reticulatis, margine subcrenulata vel undulata, plana vel anguste recurvata, supra nitida, obscure viridia, in sicco brunnescentia, irregulariter prominenti-punctata, subtus glauco-viridia, in sicco flavo-viridia, opaca, punctis minoribus nigro-punctata, pergamacea vel subcoriacea.

Inflorescentiae fructiferae tantum visae, axillares, biflorae, 7—10 mm longe pedunculatae, pedunculis puberulis, pedicelli 1—3 mm longi, puberuli. Calyx totus sub fructu persistens; tubus semiglobosus, lobi 5, triangulares, 1 mm longi. Petala non visa. Drupae subglobosae vel breviter obovatae, stylo persistente apice mucronatae, 5 mm longae, 4 mm diam., nitidae, biloculares, bispermae.

Obs.: *Rh. nipensi* Urb. affinis, quod ramis hornotinis glabris, foliis basi subcordatis, nervis lateralibus utroque latere 6—7, inflorescentia pruinosa, glabra, pedicellis 5—7 mm longis, drupa duplo majore et semine solitario bene distinguenda.

Typus: Prov. Las Villas; Sierra de Escambray, in fruticetis calcareis montanis montis Pico Potrerillo, supra opp. Trinidad, 950 m. s. m. Leg. A. BORHIDI et O. MUÑIZ, 25. V. 1970.

Clusiaceae

Clusia moaënsis Borhidi et Muñiz (Fig. 5.)

See the description of the species in l. c. p. 17.
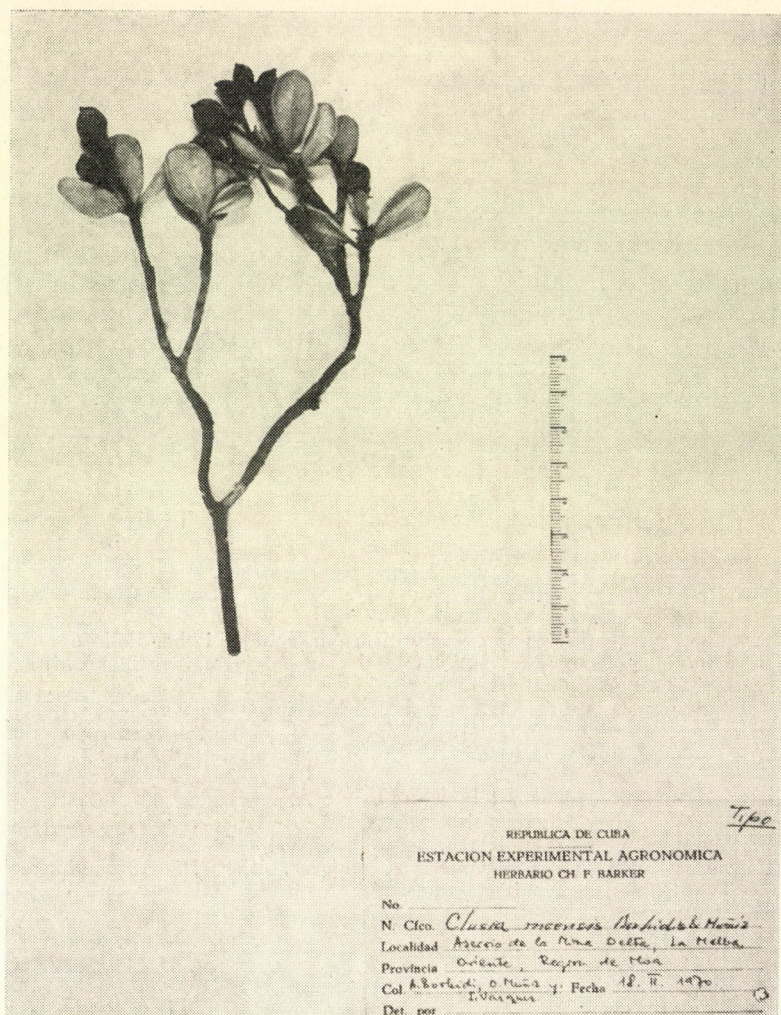
Fig. 5. Type specimen (SV 27135) of *Clusia moaënsis* Borhidi et Muñiz

Myrtaceae

Psidium acunae Borhidi (Fig. 6.)

The diagnosis of the species can be found in l. c. p. 17.

Melastomataceae

Calycogonium Susannae Borhidi (Fig. 7.)

See the description of the species in l. c, p. 18.

Fig. 6. Type specimen (LS Alain 6782) of *Psidium acunae* Borhidi
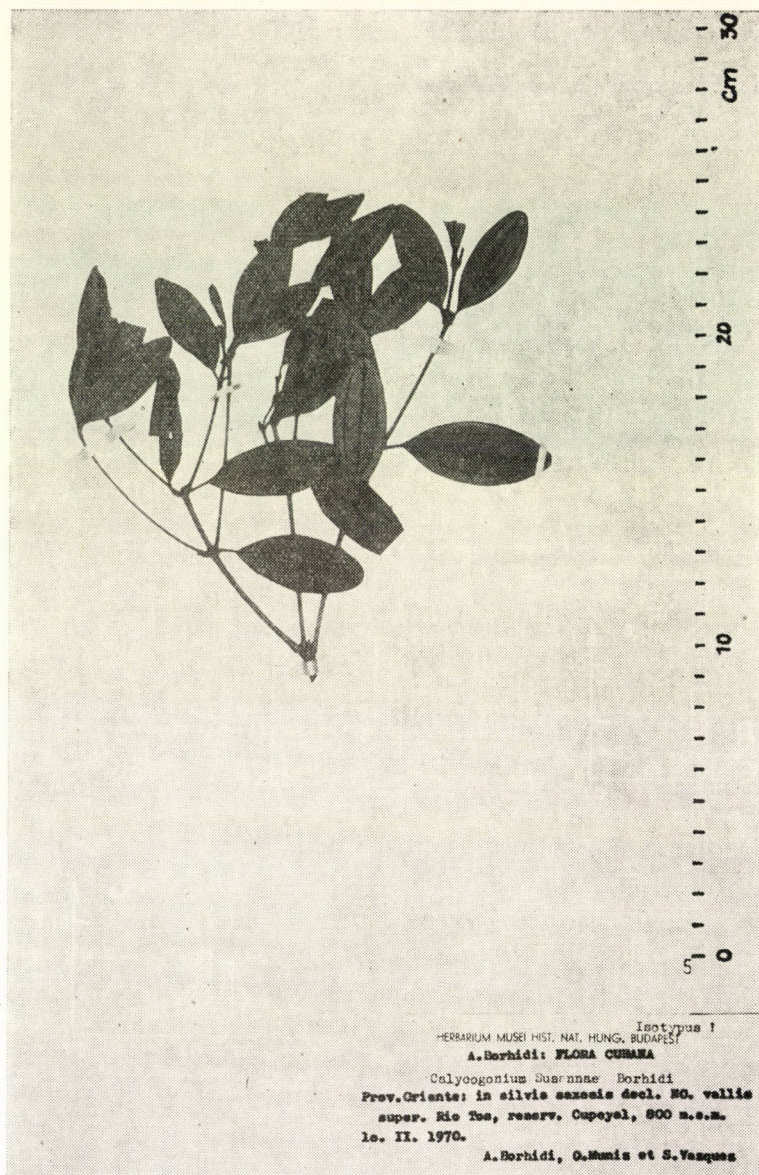
Fig. 7. Isotype specimen (Bp 503369) of *Calycogonium susannae* Borhidi

Bignoniaceae

Tabebuia petrophila Greenm. sensu Alain

1 a Folia 2—5 cm longa, apice non emarginata, margine plano; calyx 8—10 mm longus, corolla 4.5—5.5 cm longa, lobis 7 mm latis; capsula 6—7 cm

longa; prophyllis pedicelli sub calyce abeuntibus (Prov. Las Villas et Oriente) .... **T. petrophila** Greenm.

b Folia 0.5—2.5 cm longa, apice plerumque emarginata, margine recurvo; calyx 5—8 mm longus, corolla 3—4 cm longa, lobis 12—15 mm latis; capsula 3.5—6 cm longa; prophyllis pedicelli medio vel sub medio abeuntibus (Prov. Pinar del Rio, Habana et Matanzas).... **T. anafensis** Urb.

2 a Rami vetustiores ad apicem non spinescentes; folia 1—2.5 cm longa capsulae 4.5—6 cm longae (Prov. Pinar del Rio et Habana) ssp. **anafensis**

b Rami vetustiores plerumque spiniformes; folia 0.5—1.2 cm longa, capsulae 3.5—4.5 cm longae (Prov. Matanzas) .... ssp. **Munizii** Borhidi

Tabebuia anafensis Urb. ssp. **Munizii** Borhidi ssp. nova (Fig. 8)

Frutex vel arbor parva, ramosissima. Rami vetustiores teretes, glabri, strigosi, canescentes vel cinerei, apice plerumque spiniformes, hornotini cicatricibus foliorum delapsorum prominulis, internodiis inferne usque ad 1 cm longis, superne decrescentibus, ad apicem saepe subnullis et subspinescentibus, novelli densissime ferrugineo-lepidoti. Folia coriacea, ad apicem ramorum brevium valde conferta, petiolis 0.5—1.0 mm longis, cca. 0.5 mm latis, supra canaliculatis, apice non articulatis; foliola solitaria, persistentia, oblongo-elliptica, oblongo-ovata vel lineari-elliptica, basi obtusa, rotundata vel subcordata plerumque asymmetrica, apice obtusa vel rotundata, plerumque emarginata et brevissime mucronulata, 4—12 mm longa, 3—5 mm lata, nervo medio supra impresso subtus crassiuscule prominente, lateralibus (utroque latere 5—8) supra paullo prominulis subtus bene prominentibus, supra obscure, subtus conspicue reticulato-nervosa, utrinque minute et dense albo- vel flavido-lepidota, margine integro, revoluto.

Flores in apice ramorum 1—3, et in axillis superioribus solitarii; pedicelli 3—8 mm longi, medio vel sub medio prophylla bina, linearia, 1—2 mm longa gerentes; calyx campanulatus, 5—8 mm longus, in statu compresso 4—5 mm latus, basi obtusus vel cuneatus, apice bilabiatus, labiis inaequilongis, tubo 3—5-plo brevioribus, interdum apice incisis, minute et dense ferrugineo-lepidotus. Corolla 3—4 cm longa, tubus in calyce anguste cylindraceo deinde sensim ampliatus, apice in statu compresso 15—18 mm latus, lobi ampli-semiorbiculares, usque ad 12—15 mm lati. Capsula cylindrica, acuminata, 3.5—4 cm longa, 4 mm lata, brunneo-squamosa. Semina cum alis 9—10 mm longa, ipsa 3 mm magna, elliptica vel ovata.

Typus: Prov. Matanzas: Pars superior montis Pan de Matanzas, solo calcareo. Leg. O. Muñiz, 16. V. 1970. SV. Isotypus: Bp. — Prov. Matanzas: Peninsula Hicacos, Varadero, leg. Hno León et W. Seifriz 1940. VII. (León 17955, exempl. sterile).

Gesneriaceae

Rhytidophyllum mogoticola Borhidi et Muñiz sp. nova (Fig. 9)

Frutex usque ad 1—2 m altus; caulis erectus, simplex, sparse pubescens, inferne glabrescens. Folia ad apicem caulis conferta, breviter (3—12 mm longe) petiolata, oblongo- vel lineari-lanceolata, 7—20 cm longa et 3—5 cm lata, latitudine plerumque 3—5-plo longiora, apice acuminata, margine irregulariter serrulato-crenulata, membranacea, supra non vel vix subbullata, scaberulo-hirsuta, subtus hirsuta et glandulis flavis sessilibus dense disposita.

Inflorescentiae numerosae, multiflorae, folia paullo superantes; pedunculus 10—20 cm longus, dense eglanduloso-hirsutus, bracteae lineari-lanceolatae, usque ad 1 cm longae, hirsutae atque subtus glandulis sessilibus flavis obsitae, caducae. Pedicelli 1—5 cm longi, eglanduloso-puberuli. Tubus calycis globosus, inferne rotundatus, eglanduloso-pubescens, lobuli late deltoidei, 4—7 mm longi, longitudine ± aequilati, breviter acuminati, in fructu atque plerumque
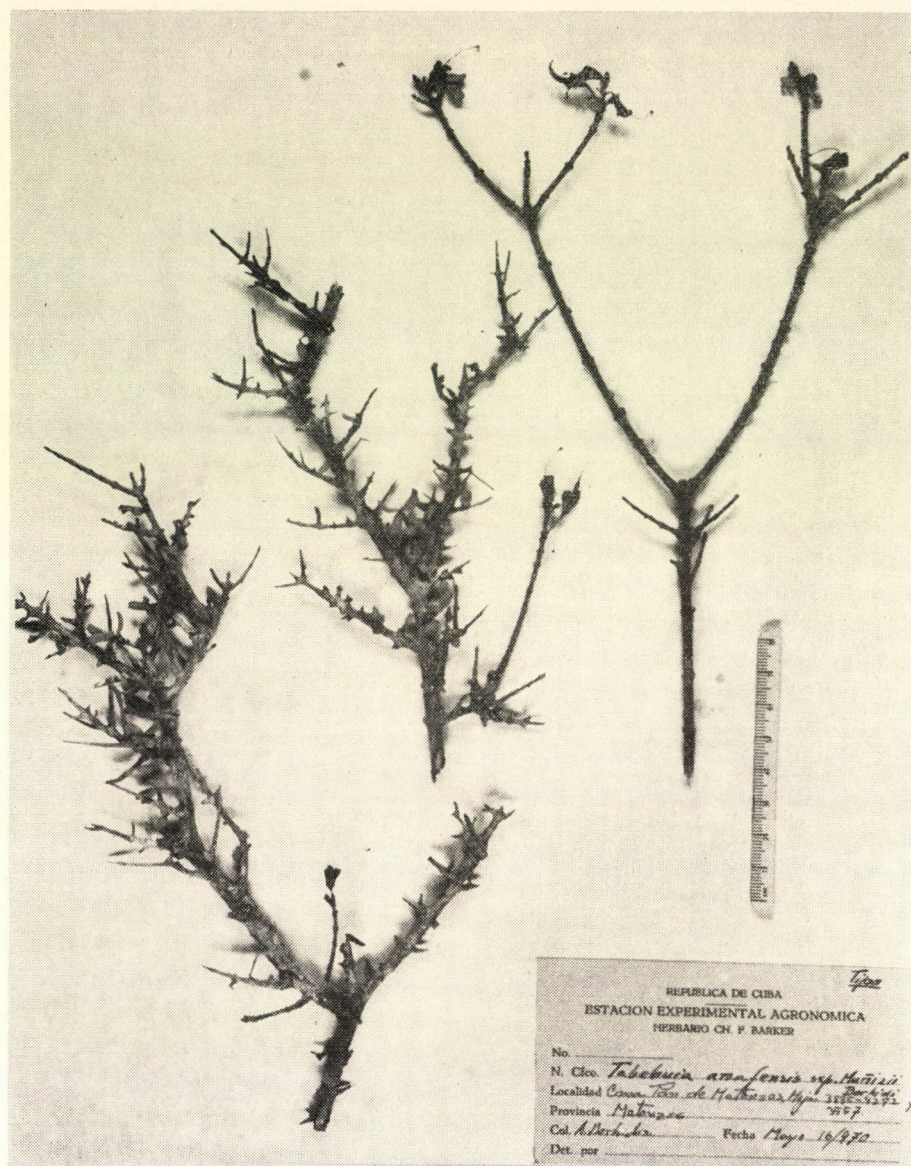
Fig. 8. Type specimen (SV sine numero) of *Tabebuia anafensis* Urb. ssp. *muñizii* Borhidi

in tempore anthesis reflexi, utrinque eglanduloso-puberuli, intus saepe purpurascentes. Corolla flavo-viridis vel purpurea, 15—20 mm longa, extus glandulis flavis sessilibus dense obsita; tubus corollae intus glaber, violaceo-maculatus. Stamina paullo exserta. Calyx fructiferus globosus, 6—8 mm diam., lobulis reflexis calycem paullo superantibus, dense pubescentibus. Fructus globosus, apice hirsutus. Semina purpurea, 1 mm longa, lineari-lanceolata, acuminata.

Fig. 9. Type specimen (SV 27121) of *Rhytidophyllum mogoticola* Borhidi et Muñiz

Obs.: *Rh. villosulo* (Urb.) Morton affinis a quo foliis paullo subbullatis, subtus glandulis flavis sessilibus glandulosis, calyce fructifero globoso, lobulis majoribus, corolla extus glandulis sessilibus obtecta valde discrepat. An species hybridogena introgressiva inter *Rh. villosulum* et *Rh. rhodocalycem* Urb.

Typus: Prov. Oriente: Sierra Maestra, in silvis humidis calcareis vallis "mogotis" inter pag. Rihito et La Tabla, 400 m. s. m. Leg. A. Borhidi, 5. II. 1970. SV 27121; isotypus: Bp.

Rubiaceae

Exostema caribaeum (Jacq.) Roem. et Schult.

var. **pubescens** Borhidi et Muñiz var. nova

A typo stipulis dense puberulis, foliis minoribus, subtus dense pubescentibus differt.

Typus: Prov. Oriente: in fruticetis calcareis siccis prope Versailles, Santiago de Cuba. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 4. II. 1970. SV. sine numero; isotypus: Bp.

Specimina examinata: Prov. Oriente: Aguadores, Santiago de Cuba, leg. A. BORHIDI et O. MUÑIZ, 20. X. 1969. — Prov. Oriente: Santiago de Cuba: El Morro, leg. J. ACUÑA et A. CORREL. — Prov. Oriente: Mesa de Lindero, inter Gran Tierra et Maisi, leg. HNO ALAIN et M. LOPEZ FIGUEIRAS.

Distributio: Litus meridionale Baracoae inter Santiago de Cuba et Maisi.

Guettarda Munizii Borhidi (Fig. 10)

See the description of the species in l. c. p. 33.

Casasia nigrescens (Griseb.) Wr. ex Urb. ssp. **moaënsis** Borhidi et Muñiz (Fig. 11)

The diagnosis of the subspecies to be found in l. c. p. 31.

Asteraceae

Heptanthus yumuriensis Borhidi sp. nova

Perennans. Folia basalia petiolis 2—5 cm longis, pilosis, ovata vel triangulari-ovata apice obtusa, basi truncata vel subcordata, 5—15 mm longa, 5—10 mm lata, profunde trilobata lobis profunde tridentatis, segmentis ovalis vel oblongo-ovatis, apice obtusis vel rotundatis, supra sparse puberula, demum glabra, glandulis sessilibus vel brevissime stipitatis dense obtecta, subtus ad nervos sparse longe pilosa, glandulis impressis punctata.

Pedunculus filiformis, 3—8 cm longus, laxe pilosus; capitulum campanulatum, 2 mm diam.; squamae involucri 5, 2.5—3 mm longae, obovato-ellipticae, pilosae, margine membranaceo-fimbriatae, fimbria squamae involucralis pilosa. Flores 9—11 per capitula; flores feminei radiales (5)-6, corolla ligulata, 3—3.7 mm longa, ligula elliptica, 2—2.2 mm longa, apice bidentata, tubo filiforme 1—1.5 mm longo. Flores bisexuales (4-)-5, corolla 5-lobata, lobis 0.5—0.6 mm longis, limbo ± aequilongis, tubus 2 mm longus. Achaenia non pleno matura 1—1.2 mm longa, sulcata, apice incrassata.

Typus: BORHIDI 673; Prov. Oriente: in saxosis humidis calcareis vallis rivi Rio Yumuri pr. pag. Sabana. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ, 20. III. 1970. Bp., isotypus: SV.

Obs.: Habitu, forma foliorum *H. lobati* Britt. affinis, qui floribus radialibus 2, ligula apice 3-dentata bene distinguenda est. *H. Shaferi* Britt. a planta nostra capitulis minoribus, 5—7-floribus, foliis margine denticulatis differt.
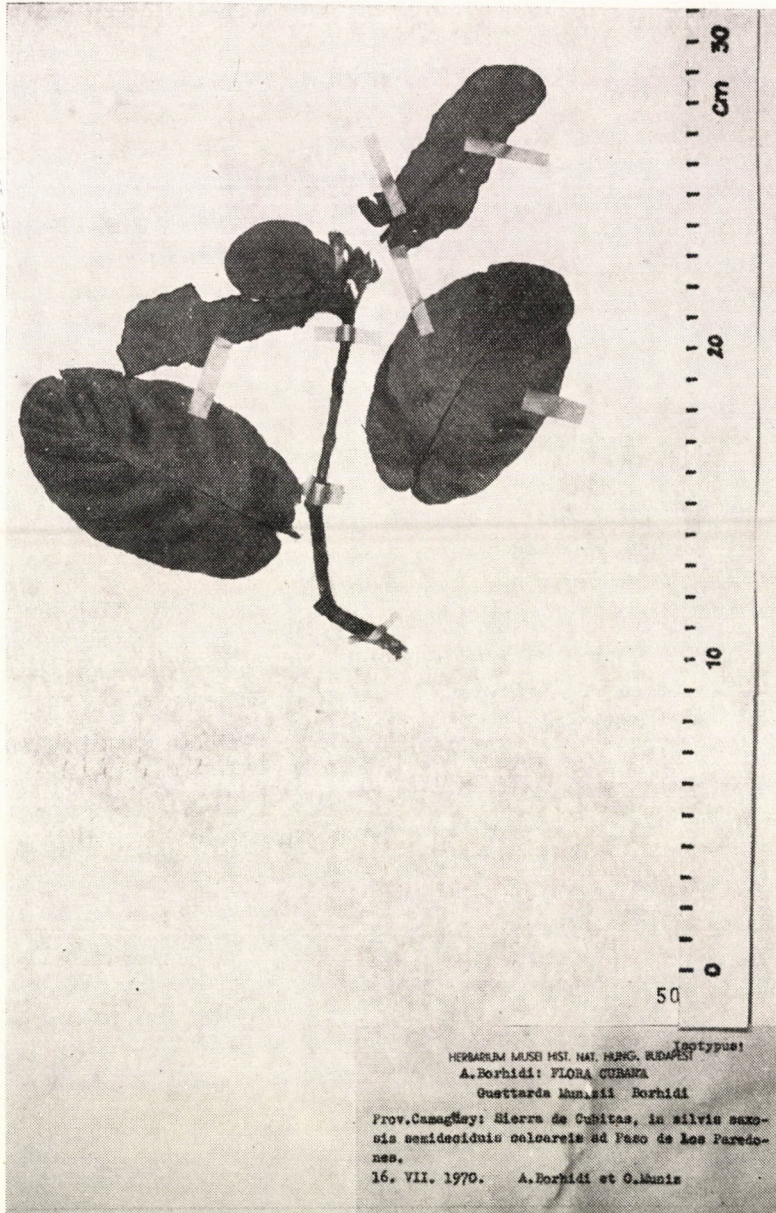
Fig. 10. Isotype specimen (Bp 503371) of *Guettarda munizii* Borhidi

Eupatorium carsticola Borhidi et Muñiz sp. nova (Fig. 12)

Frutex vel suffrutex, usque ad 1.5—2 m altus. Caulis erectus, vix ramosus albo araneoso-lanuginosus. Folia opposita vel subopposita, late triangulari-ovata, 5—7 mm longe petiolata, 2—5 cm longa, 1.5—4 cm lata, apice obtusa et mucronulata, basi truncata, rotundata vel
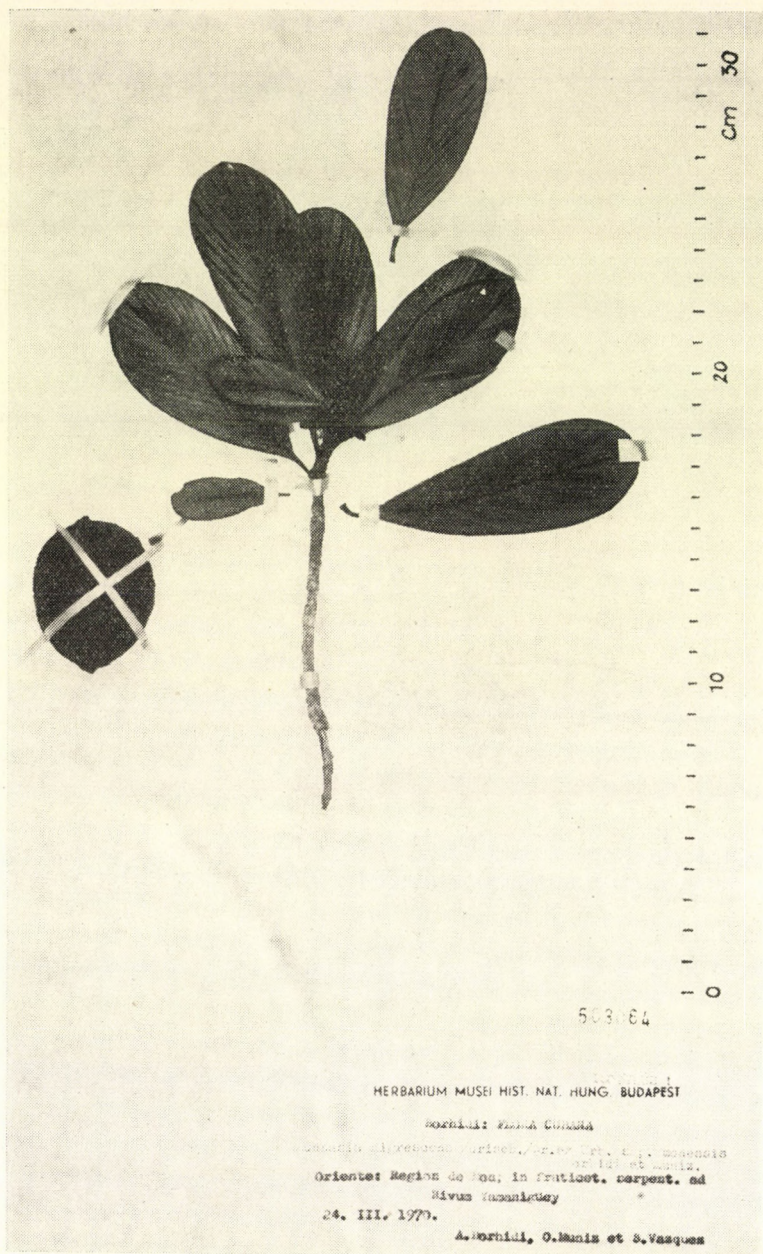
Fig. 11. Isotype specimen (Bp 503064) of *Casasia nigrescens* ssp. *moaënsis* Borhidi et Muñiz

plerumque cordata, margine crenulato-denticulata, supra in statu juvenili tomentosa, demum glabra, dense glanduloso-punctata et nervis impressis basi 3-(5)-nervia, apicem versus pinnatim disposita, conspicue reticulato-venosa, subtus densissime et permanente albo-tomentosa, nervis prominentibus et anastomisantibus reticulata.
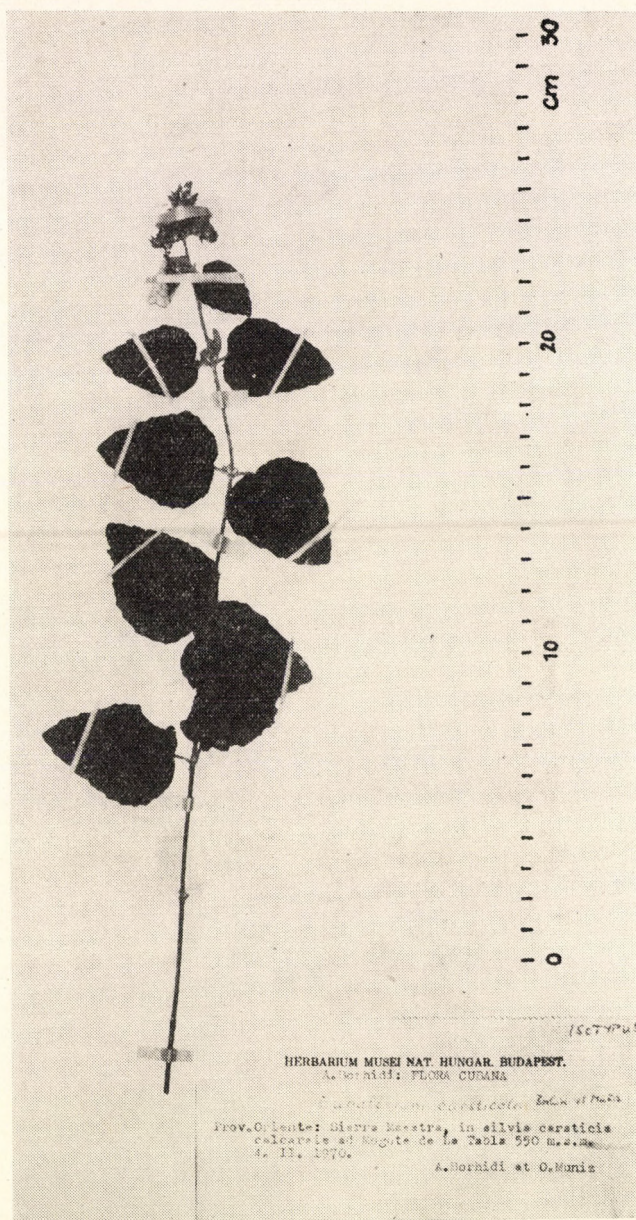
Fig. 12. Isotype specimen (Bp sine numero) of *Eupatorium carsticola* Borhidi et Muñiz

Inflorescentia terminalis, breviter trichotoma, 2—3 cm longa, capitulis sessilibus dense conferta. Capitula elliptico-ovata vel campanulata, 5—6 mm longa, albo vel grisaceo-tomentosa, 4—5 mm diam.; bracteae involucrales triseriales, exteriores ovatae, apice acutae, 2.5—3 mm longae, mediales oblongo-ellipticae, apice obtusae, 3—4 mm longae, 1—1.5 mm latae, interiores lineari-ellipticae, 4—5 mm longae, 0.6—1 mm latae, grisaceo-tomentosae. Receptaculum

glabrum. Corolla 3—3.5 mm longa, 5-lobulata, extus glandulosa, lobis subulatis, valde recurvatis, 0.5 mm longis; stylus 8—12 mm longus, corolla valde exsertus. Setae pappi 25—30, 3 mm longae, breviter pilosae, corolla ± aequilongae. Achaenia 2.5—3 mm longa, 6—7-costata, glandulosa et pilosa.

Obs.: Habitu, forma foliorum et inflorescentiae *E. plucheoidi* Griseb. affinis, quod foliis supra non glanduloso punctatis, bracteis interioribus acuminatis, achaeniis glabris bene differt.

Typus: Prov. Oriente: Sierra Maestra; in silvis carsticis calcareis ad Mogote de La Tabla in alt. 550 m. s. m. prope pag. Baire. — Leg. A. BORHIDI et O. MUÑIZ, 4. II. 1970. SV; isotypus: Bp. (sine numero).

Specimina examinata: Prov. Oriente: Baracoa meridionalis: Montecristo supra Jauco ALAIN et MORTON 5225; ALAIN et M. LOPEZ FIGUEIRAS 7021; Los Llanos ACUÑA 5021; Maisi LEÓN et M. VICTORIN; Maisi: Mesa de la Yagruma LEÓN 18229, 18340.

Vernonia praestans Ekm. ex Urb.

var. **cacuminis** Borhidi et Muñiz var. nova

A typo differt: foliis lineari-lanceolatis vel linearibus, 3—4 cm longis, 0.5—1 cm latis, apice acutis, basi trucatis vel subcordatis, margine valde revolutis; inflorescentia breve, corymbosa, capitulis ad apicem ramorum inflorescentiae confertis.

Typus: Prov. Oriente: Sierra Maestra, in pluviisilvis nebulosis muscosis montanis montis Pico Real (cacumen montis Pico Turquino) supra pag. Ocujal in alt. 1900 m. s. m. Leg. A. BORHIDI, O. MUÑIZ et S. VAZQUEZ 7. XII. 1969. SV. sine numero; isotypus: Bp.

Acknowledgement

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CYTOPHOTOMETRIC STUDIES ON THE DNA CONTENTS OF DIPLOID LOTUS SPECIES

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The author conducted comparative cytophotometrical investigations on 13 diploid *Lotus* species; in 5 of them the chromosome number is 2n = 14, while in the remaining 8 species 2n = 12. To establish the relative DNA content of the cells, the author used a type "GN 2" integrating microdensitometer (Barr and Stround Ltd., Glasgow).

The DNA absorption values of the 5 species with chromosome number 2n = 14 are higher than those of the 8 species with chromosome number 2n = 12.

The relative density value of the DNA content in the 5 species with chromosome number 2n = 14 is varying — as compared with 8 species of chromosome number 2n = 12 — between 1.48 and 2.92, in the following order: *Lotus edulis, L. arenarius, L. ornithopoides, L. requienii* and *L. cytisoides.*

Introduction

In the summer of 1971, on the invitation of Professor Dr. W. F. GRANT, I carried out cytogenetical investigations on *Lotus* species, in the Genetics Laboratory, McGill University, Montreal (Canada)*. The aim of research was to investigate the descent of species with chromosome number n:6 from species with basic chromosome number n:7, within the *Lotus* family. In connection with this problem, the caryotype of five *Lotus* species with chromosome number 2n:14 was determined (that of species with chromosome number 2n:12 had already been known; cf. R. YUNG-CHENG 1971). Examinations were carried out, with Feulgen-cytophotometric method, also for the quantitative determination and comparison of the DNA contents of 13 species with different basic chromosome numbers. The results deriving from the latter research project are submitted in the present paper.

It was SCHRADER and his co-workers (HUGHES—SCHRADER 1956—1958, HUGES—SCHRADER and SCHRADER 1956), as well as WAHRMAN and O'BRIEN (1956), who first applied cytophotometric investigations on insects. The technique has been more recently refined by RUDKIN (1967) and KEYL (1965, 1966), who made a comparison between the DNA values of the various chromosome segments and the total chromosome as well as the whole nucleus. BACHMANN

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and COWDON (1965), as well as ULLREICH (1966), conducted similar investigations on frogs. MARTIN and SHANKS (1966) examined *Vicia* species, REES et al. (1966) examined *Lathyrus*, *Vicia* and *Lolium* species, CHOOI (1971) also *Vicia* species. SOUTHERN (1967) pointed out in his cytophotometric examinations the differences in the DNA contents of the diploid, triploid and tetraploid *Tulipa* species. W. F. GRANT (1968, 1969) carried out cytophotometric examinations on *Betula* species, while GRANT and his co-worker, ROSA I. YUNG-CHENG (1971), in various *Lotus* species with chromosome number 2n:12.

Material and methods

I. Plant material

The species used in this study are listed in Table 1, with their source, area, HCN presence or absence, chromosome numbers and experimental DNA absorbance per nucleus.

II. Root tip squashes

Root tips for cytophotometric examinations were taken from plants grown in a growth chamber and greenhouse. The roots were fixed directly in Carnoy's solution (3 : 1 alcohol : acetic acid) for two hours to 24 hours at room temperature (20—24°C). Then the roots were washed in destilled water (trice), hydrolized for 10 minutes in 1N HCl at 60°C, and washed in destilled water. For staining, the root tips were placed in leucobasic fuchsin (Feulgen technique according to DARLINGTON and LA COUR, 1966) for two hours in dark, then the root tips were washed in destilled water. Maceration was carried out by placing the root tips in 4% pectinase for 2—3 hours, in order to dissolve the pection salt in the middle lamella of the cell walls without the cell contents being unduly softened, and then they were washed in destilled water. Slides were prepared by squashing root tip meristems in acetocarmine.

III. Cytophotometric comparison of the Lotus species

For a comparison of the relative nuclear DNA densities between species, with 2n : 14 and 2n : 12 chromosome numbers a standardized procedure was followed. Eight *Lotus* species, each having a 2n : 12 chromosome number—namely: *Lotus alpinus*, *L. burttii*, *L. japonicus*, *L. krylovii*, *L. palustris*, *L. pedunculatus*, *L. schoelleri* and *L. tenuis*—were used one by one as the standard species by which five species (2n : 14 chromosome numbers) — namely, *L. arenarius*, *L. cytisoides*, *L. edulis*, *L. ornithopoides* and *L. requienii* — were compared. The relative absorption of nuclei was determined by using a type "GN 2" integrating microdensitometer (Barr and Stround Ltd., Glasgow). This instrument has been established so that when cells are stained by certain methods, for example by the Feulgen method, the amount of light absorbed by the stain is directly proportional to the DNA content of the nucleus; extinction is summated as scanning progresses, so that a direct measurement of total absorption is provided in arbitrary units for a single nucleus. For DNA determinations, the chromosomes were centered within the appropriate field stop aperture for the absorption measurement and three readings were recorded. In addition, three readings of a suitable clear field (background) were also made at the same aperture. The relative absorption was obtained by subtracting the average of the three background readings from the average object reading. The telophase stage (2C) was used for all measurements. (2C is customarily designated for the DNA value of a nucleus before DNA synthesis has occurred.) A total number of determinations was 30 chromosome fields for each individual species. Absorption was measured with the integrating microdensitometer at a wavelength of 550 mμ. All measurements were made with 45 × oil immersion objective, and on the absorption range 20.

Results and discussion

CHOOI (1971) examined the relative DNA contents of telophasic dividing cells of 45 species belonging to 4 sections of the genus *Vicia*; in making a comparison between them, he found distinct differences between the species

of the sections. GRANT and ROSA I.-YUNG determined the nuclear DNA content of 10 *Lotus* species (chromosome number 2n = 12) and of several hybrids with the cytophotometric method. They found that the mean DNA per 2C values for the nucleus ranged from 1.750 – 2.120, while the mean DNA values for the hybrid ranged from 1.825 to 2.255 units. The statistical analysis of the values of 2C nuclei between *Lotus* hybrids indicated these differences to be non-significant. The authors pointed out an interrelation between DNA content, caryotype, chromosome number and the diameter of the nucleus. The DNA value relating to one chromosome depends also on the dimensions of the chromosome. A similar observation was made by GRANT (1969) in the case of *Betula* species. In the course of ploidization, with the increase in nuclear diameter DNA absorption generally increases, while the mean of DNA per chromosome decreases.

The DNA absorption mean values of the telophasic chromosome section of the 5 *Lotus* species with 2n = 14, and of the 8 species with 2n = 12 chromosome numbers, examined by me, are given in Table 1. The order of sequence, from the species with lower DNA absorption values to the higher ones — in the species with chromosome number 2n = 14 — are as follows: *L. edulis*, *L. arenarius*, *L. ornithopoides*, *L. requienii* and *L. cytisoides*, with ratios of 1 : 1.01 : 1.16 : 1.21 : 1.25. In the various species merely a small difference appears between the extreme values, viz. 1.66. The order in the case of species with 2n = 12 chromosome are as follows: *L. alpinus*, *L. japonicus*, *L. krylovii*, *L. burttii*, *L. tenuis*, *L. pedunculatus*, *L. schoelleri* and *L. palustris*, with ratios of 1 : 1.07 : 1.10 : 1.11 : 1.33 : 1.44 : 1.58. The difference between the lower and higher values of these species appears also only as 1.61. Deviation in the DNA absorption values is higher in the case of *Lotus* species with 12 and 14 chromosome numbers, viz. 3.50—3.42.

The cell-related values of relative DNA content of the 13 *Lotus* species are given in Fig. 1. (The ordinate represents the relative DNA content per cell, the abscissa represents the various species.) The DNA content of *Lotus* species with chromosome number 2n = 14 produce values between 5.56 and 8.78, while that of species with chromosome number 2n = 12 is between 12.94 and 16.26. The average was taken from the measurements of 15 cells in each species.

The relative absorption values of the various species are given in six diagrams, on the basis of 30 measurements. The values of the species with chromosome numbers 2n = 12 and 2n = 14 are given side by side in the diagram, from the lower towards the higher values. In *Lotus* species with chromosome number 2n = 14 the values were higher in every case than in species with chromosome number 12 (see Figs 2—7); *L. arenarius :* 5.4—7.5, *L. cytioides :* 6.5 — 1 0.0, *L. edulis :* 5.0 — 8.5, *L. ornithopoides :* 5.5 — 9.3, *L. requienii :* 66—9.0, *L. alpinus :* 2.0—3.6, *L. burttii :* 2.3—4.5, *L. japonicus :* 2.5 —4.0,

L. krylovii: 2.5—3.8, *L. palustris:* 3.4—5.8, *L. pedunculatus:* 2.8—4.8, *L. schoelleri:* 3.0—4.6, *L. tenuis:* 3.0—4.5.

The relative densities of the DNA contents for the section with telophasic chromosome were compared in the case of 13 species, so that the species with chromosome number 2n = 12 (one by one) were taken as standard values, and they were compared with the values of the species with chromosome number 2n = 14. The value of the standard species is 1.0 in every case. The relevant results are given in Table 2.

The DNA density values of the five *Lotus* species with chromosome number 2n = 14 — in a comparison with eight *Lotus* species of chromosome number 12 — are as follows: *L. edulis* 1.48—2.32; *L. arenarius* 1.49—2.36; *L. ornithopoides* 1.77—2.72; *L. requienii* 1.78—2.81 and *L. cytisoides* 1.85—2.92.

Table 1

Acc. No.	Species	Source
B-570	*Lotus arenarius* Brot.	Spain P. I. 303948, Northeast Regional Plant Introduction Station, Geneva, N. Y.
B-265	*Lotus cytisoides* L.	Division of Plant Industry Camberra City, A. C. T. Australia
B-96	*Lotus edulis* L.	C. P. I. Australia, No. 14524; in Algeria, coll.: J. F. MILES
B-268	*Lotus ornithopoides* L.	Botanischer Garten der Karl-Marx Universität, Leipzig (Germany)
B-270	*Lotus requienii* Mauri	Estaca Romonica Nac Nal Savem (Port.)
B-77	*Lotus alpinus* Schleich.	Swiss Alps: Valley of Emaney, coll.: C. FAVAGER
B-303	*Lotus burttii* Sz.—Borsos	Bank of Kabul river Peshawar (Pakistan) coll.: B. L. BURTT (Royal Botanic Garden, Edinburgh)
B-129	*Lotus japonicus* (Regel) Larsen	River bank, Gifu (Japan), coll.: I. HIRAYOSHI
B-86	*Lotus krylovii* Schischk. et Serg.	Hortus Botanicus Universitatis Uppsala
B-115	*Lotus palustris* Willd.	Government Agricultural Experiment Station. Naveh-Yaar (Israel), coll.: S. GALLILEA
B-89	*Lotus pedunculatus* Cav.	U. S. Dept. of Agriculture, Belstville, Maryland coll.: P. HENSON
B-166	*Lotus schoelleri* *Schweinf.*	Grassland Research Station Kitale (Kenya)
B-145	*Lotus tenuis* W. et K.	U. S. Dept. of Agricultural, Soil Conservation Service, Pleasanton (Calif.)

On taking the mean of the absorption values of the examined species with chromosome number 12 as standard (1.0) and, in comparison with the species of chromosome number 2n = 14, the values of the relative density from the lower towards the higher ones are as follows: *L. edulis* 1.87; *L. arenarius* 1.90; *L. ornithopoides* 2.18; *L. requienii* 2.26 and *L. cytisoides* 2.36.

In the individual histograms (Fig. 8) the relative density values of the DNA content of five *Lotus* species with chromosome number 2n = 14 are represented (on the basis of 30 measurements in each species) in relation with the mean of the eight *Lotus* species with chromosome number 2n = 12 (in the case of arbitrary units). In this way, the order of species and their extreme values are as follows: *L. edulis* 1.45—2.46; *L. arenarius* 1.56—2.10; *L. ornithopoides* 1.59—2.69; *L. requienii* 1.91—2.61 and *L. cytisoides* 1.88—2.89.

HCN	Area	Chromosome number (2n)	Experimental DNA absorbance of telophase stage per nucleus
+	Spain, Portugal, Canary Isl., Madeira, Marocco	14	6.55
?	Omni-Mediterranean	14	8.13
+	Mediterranean: northward to Provence and to Golf of Quarnero	14	6.47
+	Mediterranean: from Spain to Asia Minor — Caucasus, northern: Riviera to Istria, Canary Isl.	14	7.55
+, —	Omni-Mediterranean	14	7.81
+	Europa (Iberian Penins., Pyrenees, Alps, Balkan Penins., North- and Northeastern Carpathians), Africa North, West-Asia to Himalaya. (On high mountains)	12	2.78
—	Pakistan	12	3.09
+	Japan, Korea, Eastern China, Taiwan	12	2.97
—, +	Westasiatic species: West-Asia eastern to East Europa	12	3.07
—	East-Mediterraneum — to Asia Minor, Caucasus (West Transcaucasian)	12	4.39
—	West-Mediterranean endemic species. West-Mediterranean: Spain, South-Portugal (?Marocco)	12	3.71
—	Tropic. Africa: Ethiopia, Sudan, Eritrea, Kenya, Tanzania	12	4.00
+, —	European species, mainly: South- and Central-Europa, eastward to West-Asia: Turkestan, Afghanistan, Dsungaria	12	3.59
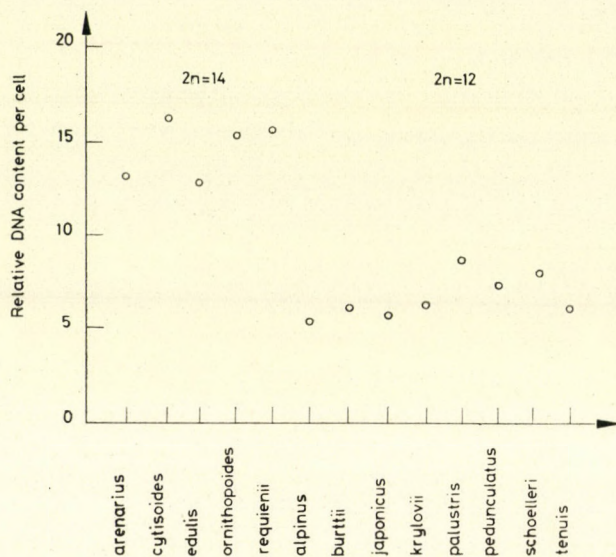
Fig. 1. Graph showing the distribution of relative DNA content per cell of 13 species of diploid *Lotus*
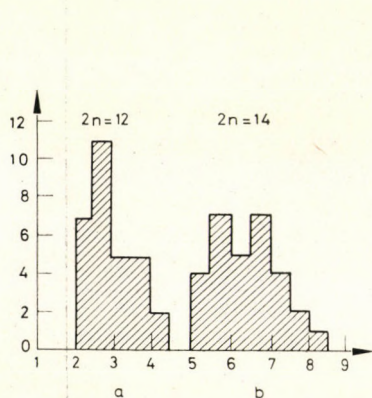
Fig. 2. Lotus burttii, b. *Lotus edulis*
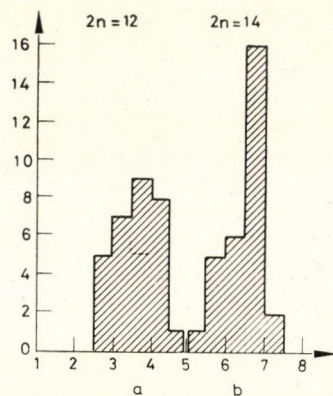
Fig. 3. Lotus pedunculatus, b. *Lotus arenarius*

Fig. 2—7. Frequency diagrams of Feulgen absorption measurements in nuclei of species with chromosome number 2n = 12 and 2n = 14. (The ordinate represents the number of nuclei measured; the abscissa represents the relative absorption value of DNA.)
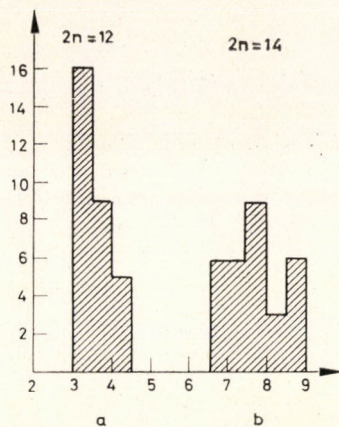
Fig. 4. Lotus tenuis, b. *Lotus requienii*
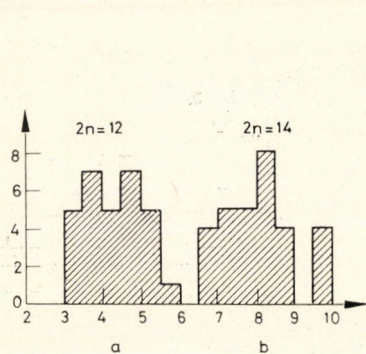
Fig. 5. Lotus palustris, b. *Lotus cytisoides*
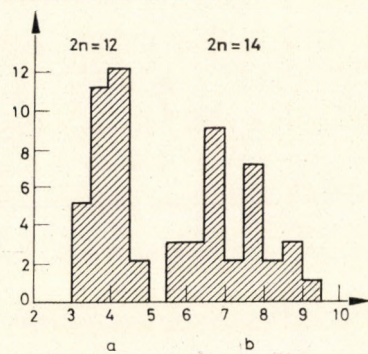
Fig. 6. Lotus schoelleri, b. *Lotus ornithopoides*
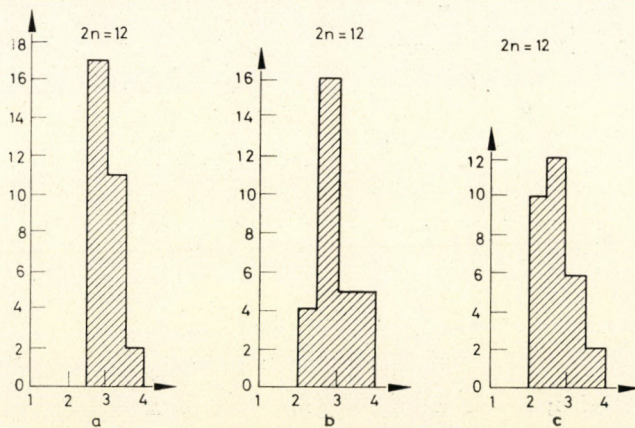
Fig. 7. Lotus krylovii*, b. *Lotus japonicus*, c. *Lotus alpinus

Table 2

Relative DNA content for 2C nuclei (in arbitrary units) of Lotus species, relative to absorbance of standard (2n = 12) given the value of 1.0

Standard species (2n = 12 chromosome number)	Species with 2n = 14 chromosome number				
	arenarius	*cytisoides*	*edulis*	*ornithopoides*	*requienii*
L. alpinus	2.36	2.92	2.32	2.72	2.81
L. burttii	2.12	2.63	2.09	2.44	2.53
L. japonicus	2.13	2.65	2.11	2.46	2.54
L. krylovii	2.20	2.74	2.18	2.54	2.63
L. palustris	1.49	1.85	1.48	1.72	1.78
L. pedunculatus	1.76	2.19	1.74	2.03	2.10
L. schoelleri	1.64	2.03	1.62	1.88	1.95
L. tenuis	1.82	2.26	1.80	2.10	2.17
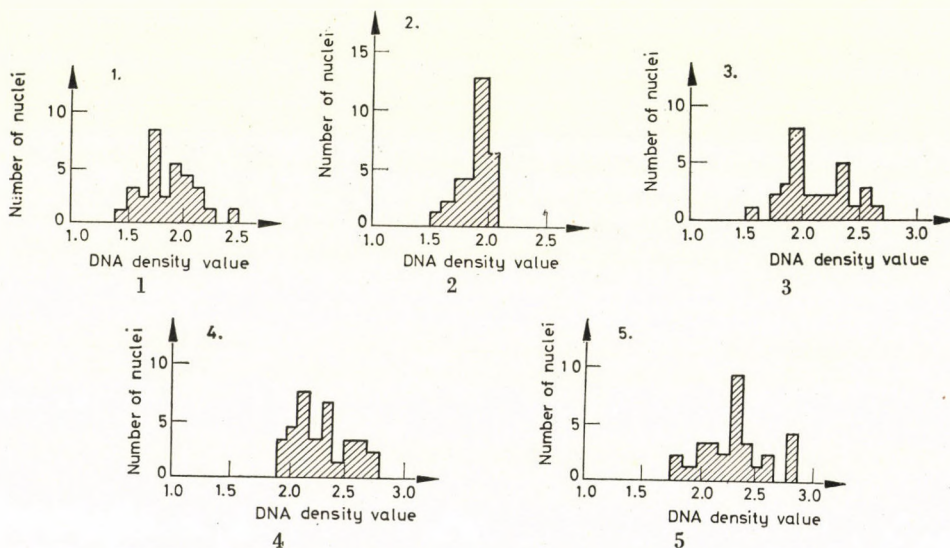
Fig. 8. Histograms of DNA amounts in 2C nuclei of *Lotus* species with somatic chromosome number 2n = 14. 1. *Lotus edulis*, 2. *L. arenarius*, 3. *L. ornithopoides*, 4. *L. requienii*, 5. *L. cytisoides*. (The ordinate represents the number of nuclei measured; the abscissa represents the relative density of DNA, in arbitrary units.)

Summary

1. Comparative cytophotometric examinations were carried out in 13 diploid *Lotus* species; 5 species had chromosome number 2n = 14, 8 had 2n = = 12. For determining the relative DNA content of the cells, a type "GN 2" in-

tegrating microdensitometer was used. Dividing cells from the root tips of each of the Lotus species examined were used for the measurements, in telophasis (telophase stage, 30 chromosome fields).

2. For determining the relative density of the nuclear DNA content, the relative absorption values of the DNA content of species with chromosome number 14 were compared with those of each of the species with chromosome number 12; also the DNA absorption values of each of the species with chromosome number 2n = 14 were compared with the mean of the DNA absorption values of all species with chromosome number 2n = 12. The order of the species with chromosome number 2n = 14, from the lower values towards the higher ones, is as follows: *L. edulis*, *L. arenarius*, *L. ornithopoides*, *L. requienii* and *L. cytisoides*.

*

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LEAF ANATOMICAL AND PHOTOSYNTHETICAL REACTIONS OF QUERCUS PUBESCENS WILLD. TO ENVIRONMENTAL FACTORS IN VARIOUS ECOSYSTEMS

I. LEAF ANATOMICAL REACTIONS

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The ecological inquiry of this work concerns the changes taking place in the rates of four anatomical characteristics in the leaves of *Quercus pubescens*, under the influence of environmental factors. Two levels of light and water supply and, from the combinations of these, four habitat types were selected.

The rate of palisade per spongy parenchyma and the size of the mesophyll chambers react in the same way to the combinations of the two factors. The effect of light alone on the rate of palisade per spongy parenchyma is significant; while on the size of mesophyll chamber each of the two factors has a significant influence; on the intercellular rate and stoma frequency only the effect of the water factor is significant in itself. At a lower level of light intensity the leaf anatomical characteristics are more stable against the effects of the water supply of the soil than under more intensive light conditions. The intercellular rate is correlated with the size of mesophyll chambers and with stoma frequency.

In the authors' opinion, the mesophyll chamber can be conceived of not only as a unit of gas supply but also as the unit producing and transporting organic matter.

Introduction

Quantitative phytocenological observations — in the mountains of Buda — as well as production ecological investigations — in the PP section of IBP — have been carried out for years in xerothermic seed-producing oak-woods. Concerning the wood production (size, diameter, etc.) of the dominating oak species, *Quercus pubescens*, examples of nearly the same age show a considerable variability (according to plant communities and, within this, to ecological factors) even within a small area. So the question concerned with the ways and means of ecological influence has arisen, and concretely, whether the influence of ecological factors can be measured on the anatomical characteristics of the leaf, the main organ of CO_2 assimilation, as well as on the capacity of the leaf to incorporate CO_2, and whether there is a relation between anatomical structure and function?

In this paper the results of the functional-anatomical approach are dealt with. (The ability to assimilate CO_2 will be discussed in the next paper.)

A great number of studies treat the question of the functional-anatomical characteristics of the leaf, especially of the change in stoma frequency ac-

cording to habitat type. In the present study the effects of the ecological-habitat factors on identical individuals and on 4 different anatomical characteristics are measured and evaluated.

Material and method

For the right selection of experimental plant individuals, the examination of the two most important factors of *Quercus pubescens* habitat types had to be carried out before the collecting of experimental plant material. The two chosen factors were light supply and water supply; the measurements related to them and their evaluation should be considered preliminary investigations (subsection a), as against subsection(b), where the description of measurement methods for the investigation of the plant is presented.

(a) Viewpoints of selecting the sample trees (preliminary investigation of environmental factors)

In the sampling area, on the southern side of the Remete Hill in the Buda Mountains, *Quercus pubescens* can be investigated in its whole phytocenological range, from Turkey oakwoods (*Quercetum petraeae-cerris*) to karstic hair oak bushwood (*Ceraso-Quercetum pubescentis*). According to previous information, the growth of the tree species is considerably controlled by the water supply, that is, the water capacity of the soil (factor b) closely correlated with its depth. Another significant factor, related to CO_2 assimilation, is light supply (factor a). The sample objects (sample trees) were marked also on the basis of these two factors so that two levels of both factors were chosen. The four combinations of factors thus formed occur extensively in the area. Three sites and three sample trees of each factor combination (=habitat type) were chosen as repetitions. This selection was based on preceding light measurements and soil investigations. The low level of light is characteristic of the first two habitat types ("little light", a_1), while a higher level of light ("much light", a_2) is characteristic of the other two. Selection according to light was carried out on 30 July, 1970 (thus in the completely developed state of the foliage) on the basis of measuring light every two hours. Measurements taken in lux at 1.5 m under the sample trees were considered acceptable for the shade leaves of the foliage (cf. TRANQUILLINI 1960), although the shade leaves were at 3—7 m height. Light measurement at 6 a.m. is characteristic of the morning and before-noon light conditions.

Table 1

Data of light measurements in at 6 a. m.; 10^3 lux, on 30 July, 1970

Habitat type	1	2	3	Average
1	0.279	0.465	0.558	0.434
2	0.465	0.558	0.558	0.527
3	1.023	1.116	0.930	1.023
4	0.837	1.488	1.860	1.395

Table 2

Analysis of variance on the data of Table 1

Source of variability	SQ	df	Ms
Treatment	1.813	3	0.604*
Error	0.599	8	0.075
Total	2.412	11	

Significance levels: *P = 5%, **P = 1%, ***P = 0.1% in all tables.

Table 3

Averages of light intensity values, their differences and levels of significance (30 July, 1970, 6 a. m.)
(Mean values are diagonal, their difference in the top right-hand corner, their significance level in the bottom left-hand corner)

X: P = 5%; XX: P = 1%; XXX: P = 0.1% in all tables

Habitat type	1	2	3	4
1	0.434	0.093	0.589	0.961
2		0.527	0.496	0.868
3	X		1.023	0.372
4	XX	XX		1.395

Up to 10 a.m. largely similar differences existed in the light conditions. Post noon, no reliable difference could be demonstrated between the third and the first two habitat types. After this — until 5.30 p.m. — the fourth habitat type separates in all measurements even from the third, with light intensity values saliently high against also the latter. However, considering the duration of light, the third and fourth habitat types separate from the first two well.

As the structure adequate to the function is induced by the habitat factors at the time of growth of the organs, the light measurements in our sytem were carried out also during the spring, on 3 May, 1971, at the stage of leaf growth. The leaves at that time were still undeveloped (they extended to some half of the later total area) and showed intensive growth. The data of measurements at 9 a.m. will be taken out and evaluated.

Table 4

Light intensity values in 10^3 lux, at 9 a. m. on 3 May, 1971

Habitat type	1	2	3	Average
1	5.86	4.60	4.65	5.036
2	4.58	3.56	3.72	3.953
3	7.25	8.37	7.44	7.686
4	11.16	10.23	11.16	10.850

Table 5

Analysis of variance

Source of variability	SQ	df	MS
Treatment	85.124	3	28.374***
Error	2.916	8	0.364
Total	88.040	11	

Table 6

Averages of light intensity values, their differences and levels of significance (9 a. m. on 3 May, 1971)

Habitat type	1	2	3	4
1	5,036	1.083	2,650	5,814
2		3.953	3.733	6.897
3	XXX	XXX	7.686	3.164
4	XXX	XXX	XXX	10.850

These measurements suggest the separation according to light of the first two habitat types from the third and fourth habitat types, and even more so than the measurements carried out at the time of the completely developed foliage state. The fourth habitat type separates in the morning from the third also in the spring. Regarding however, the noon — early afternoon light intensity, the fourth habitat type fails to exceed as considerably as during the summer when the more developed foliage and shade of the trees of the first three habitat types create considerable contrasts in the comparison of habitat types. On the other hand, the cause of greater morning light differences induced by the exposition is the scarcely developed foliage of the neighbouring trees, admitting also lateral light.

The type of the soil refers satisfactorily to water supply (for the detailed soil physical — soil chemical conditions and experimental methods, see SZUJKÓ-LACZA and FEKETE 1971) The first and third habitat types were designated as b_1 ("much water"), since deep, Ramann's brown forest soils developed here on loess or clay; the limestone rock-bed lies 90—130 cm deep. The soil consists of about 30 cm deep humus layer and of 60—100 cm clayey-adobe, water-storing B-level. The second and fourth habitat types are characterized by 30—45 cm deep, black and brown rendzinas, in which the humus and limestone fragments are more considerable; accordingly they are A—C level soils (cf. STEFANOVITS 1963). The thickness and water capacity of the arable soil layer does not extend to even half of those in Ramann's brown forest soil, so these are characterized by "little water" (b_2). Thus the habitat types in sequence are: 1. (a_1b_1), 2. (a_1b_2), 3. (a_2b_1) and 4. (a_2b_2).

In assigning the habitat type from the point of view of water regime, the criterion of the relative humidity of the air could, in principle, also be taken into consideration. Preference was given to water capacity of the soil, because the preliminary examinations (FEKETE and SZUJKÓ-LACZA 1971) pointed out a relationship between the hygroscopic water-binding ability of the soil and the undergrowth in the sample area.

In the first habitat type, *Quercus pubescens* occurs in a lower frequency, since other species (mainly *Quercus petraea, Quercus cerris*) are stronger competitors here. The phytocoenosis is a transition between *Quercetum petraeae-cerris* and *Orno-Quercetum*. The second and the third habitat types are the coenological centre of the hair oak: the *Orno-Quercetum* (*Oryzopsis virescens* or *Vicia sparsiflora* type; cf. PRÉCSÉNYI—FEKETE—SZUJKÓ-LACZA 1967). The fourth habitat type coenologically means an extreme occurrence (karstic hair oak bushwood (*Ceraso-Quercetum pubescentis*). In the second and fourth habitat types only *Fraxinus ornus* is a considerable competitor. For the characteristics of the associations mentioned, see ZÓLYOMI (1958).

(b) Anatomical examinations and the methods of evaluation

From 12 sample trees of the four habitat types leaf samples were taken by the end of August, 1970. The leaves originated from the lowest thick branch of each sample tree, having been top leaves on top shoots, to be regarded as shade leaves within the canopy of the given tree. (When choosing the leaf insertion, the statement of POLSTER, WEISE and NEUWIRTH, 1960, was not indifferent; they pointed out, concerning *Quercus cerris* growing in similar habitat types, that the leaves most active in the diurnal cycle of photosynthesis lie in the lowest position.) — Half of the collected material underwent leaf anatomical, while the other half physiological examinations.

The fresh weight and the surface of the leaves (5 in each case) were determined (by optical planimeter); the quotient of these two values is the density thickness (MCCLENDON 1962). The generally known variability of the stoma frequency, occurring also within one leaf namely the error within one sample, was minimalized so that by a preliminary counting it was established that the stoma number for unit area shows the smallest variability in the area

between the second and third or between the third and fourth lateral veins of the midrib, counted from below. (Similar sampling, taking the sample from the same leaf area was applied by PISEK, KNAPP and DITTERSTORFER 1970). So the counting of stomata was concentrated to this place (counting from 10 collodion proofs per each sample tree). For the measurement of the various tissue layers, the leaves were fixed in Navasin solution, embedded in paraffin, and stained in toluidin blue. From the intersections near the midrib, cross-sections of 15—20 μ were prepared (SÁRKÁNY and SZALAI 1957). The paradermal sections were hand-cut sections of fresh leaves, which were immediately microphotographed. The rate of the assimilating tissue layers of the mesophyll was obtained by measuring under the microscope the thickness of the palisade parenchyma layer, on the basis of 10—20 leaf cross-sections per sample tree, and relating it to the thickness of the whole mesophyll. Since in the layers measured in this way the intercellulars were also included, another method was also applied, viz. the leaf cross-sections were photographed; the negatives projected on white paper, the various layers traced along the borders of the cells, then cut out and the surface of the various layers (palisade parenchyma, spongy parenchyma, layer of the collecting cells, ribs and intercellulars) was determined by optical planimeter. The rate of palisade parenchyma per spongy parenchyma as well as the rate of intercellulars per assimilating tissues (=intercellular-rate) were determined by this method. Finally, the areas closed by the bundle sheath extensions surrounding the ribs on the epidermis were measured on colloidal proofs; these values were multiplied by the thickness of the mesophyll, thereby calculating, by 25 measurements for each sample tree, the general volume of the so-called mesophyll chambers.

The influence of the habitat type on the individual elements of the leaf structure was evaluated by two-factorial, two-level analysis of variance. For the establishment of relationships between anatomical characteristics, correlation calculation was applied (SVÁB 1967).

Results

The leaf anatomy of Quercus pubescens

Since the leaf anatomical description of *Quercus pubescens* could not be obtained from the literature, similarly as in the case of the preliminary investigations into the environmental factors, the qualitative examination and description of the leaf became necessary.

On the top shoots of *Quercus pubescens*, the leaves grow by fives or more rarely by sevens, on the lateral shoots by threes and fours. The leaves are lobed, pubescent, with 5—7 pairs of lateral veins decurrent from the midrib.* The lateral veins are also starting points for ramifications of the third, fourth, etc. order. The anastomosing veins eventually divide the mesophyll into cells.

Starting from the petiole, the distance between the lateral veins increases (Table 7).

The angle subtended by the midrib and the lateral veins, starting also from the petiole, decreases (Table 8). The cell dividing ability of the meristematic submarginal epidermis and its cell dimensions influence the extension of the intercostal regions.

The base of the leaf (pulvinus) is slightly swollen and continues in the petiole. The petiole is semicylindrical, flattening on the dorsal but semicircular on the ventral side. The continuation of the petiole is the midrib of the leaf,

* An elaboration of the leaf morphology of the species is being carried out by V. MÁTYÁS; in the following sections reference to the external morphology is given only if the anatomical description requires it.

Table 7

Distances between the neighbouring primary lateral veins on the midrib in Quercus pubescens (mm, in five repetitions)

Lateral vein pairs (numbered from the petiole)	1	2	3	4	5
1—2	2	6	2	2	4
2—3	5	6	10	5	4
3—4	9	9	12	9	11
4—5	10	12	13	12	14
5—6	12	14	16	13	14
6—7	17	—	14	—	—

Table 8

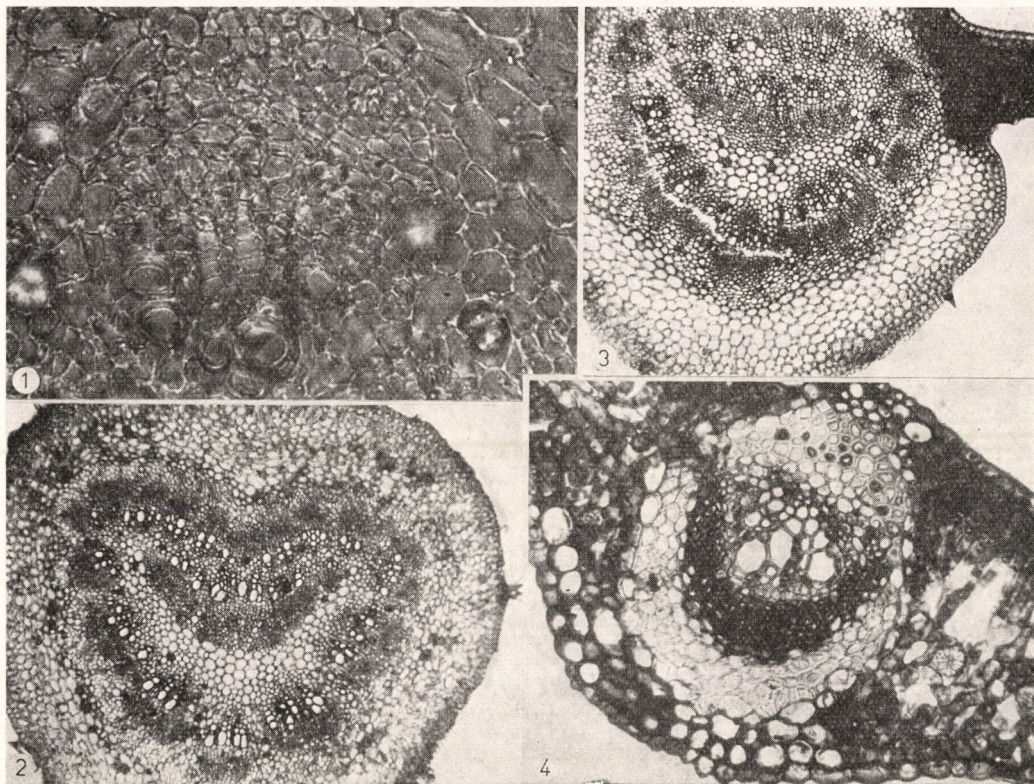
Angles subtended by the primary lateral veins and the midrib measured towards the tip, in the Quercus pubescens leaf (data of five leaves)

Serial number of lateral vein (starting from the petiole)	1	2	3	4	5
1.	71	68	74	71	62
2.	58	74	62	66	53
3.	52	63	62	51	32
4.	38	60	55	42	33
5.	17	43	44	16	19
6.	12	30	26	—	—
7.	—	—	19	—	—

keeping its bifacial character. The main and the lateral veins lie in the plane of the leaf blade, or occasionally slightly sunk in the mesophyll, while on the underside of the leaf they protrude from the mesophyll.

Leaf base (pulvinus)

Under its epidermis cells and embedded in the parenchymatous tissue, a collateral open bundle, arranged in semicircular arch, enters the base of the leaf from the shoot axis. In the collateral open bundles, the phloem lies towards the ventral epidermis, the xylem towards the axis. There is parenchymatous tissue between the vascular bundles. In the parenchymatous tissue cells of the leaf base there is little chloroplast, while in the cells produced usually by equal division (but later also in the single parenchyma cells) there are calcium oxalate druse crystals (Photo 1).

Plate I. 1. Isolated vascular bundle from the base of leaf. ×580. 2. Transporting bundle system pattern in the petiole. ×80. 3. Midrib in the leaf blade. ×80. 4. Lateral vein with reduced phloem elements from the upperside of the leaf. ×670

The transporting bundle system of the petiole and the leaf blade

Two kinds of hair type can be found on the hair basis cells among the epidermal cells on the surface of the petiole: branched hairs, and the rather rarely occurring, secretory gland hairs with a club-shaped head. In the direction from the epidermis towards the axis, the form of the parenchyma cells of the ground tissue under the epidermis changes. The diameter of these cells increase radially to the axis in the cross-section. (Later the two cell rows under the epidermis in the petiole develop into a thicker-walled hypodermis.) The following (about) 10 cell rows consist of cells containing also chloroplast, but a number of plastid-less cells also occur among them. The cells of the 13th and 14th cell rows are tangentially slightly elongated. In the 15th and 16th cell rows green plastids are amply found. The cells of these radially dividing and elongating cell rows, richer in plastids, subdivide the vascular bundle system to

be described below. In certain cells of the innermost cell row there are crystals instead of plastids. These cells are in contact with the fibre bundle sheath, which is slightly concave on the dorsal side but considerably vaulted on the ventral side within which the fibre bundle sheath is divided into further, usually 9, smaller vaults by the parenchymatous cells of the ground tissue mentioned before. These fibre arches are adaxially in contact with the phloem part of the same division. The phloem is followed, until the complete development of the leaf by a bi — to triseriate cambium, then by the first xylem. The xylem, designable as No. 1 and divided into archs, is in contact adaxially with a contiguous layer of parenchymatous ground tissue consisting of a few rows of cells. The hollow side of the uniformly lunate parenchymatous ground tissue is in contact with another phloem part (No. 2) adhering to the lunate shape, with another subsequent cambium and the No. 2 xylem running axially towards the dorsal epidermis. The parenchymatous cells of xylem No. 2 are in contact with the parenchymatous cells of the xylem of the vascular bundle decurrent from the dorsal direction. This third xylem is followed by the third cambium and phloem No. 3, in contact with the fibre ring formed from the dorsal side (Photo 2).

The petiole continues in the midrib where the distribution of the transporting elements is the same up to the first lateral vein of the leaf blade (Photo 3). From here, the number of the transporting elements decreases up to the top of leaf blade.

The decrease results in the gradual disappearance of phloem and xylem No. 2, together with the central layer of parenchymatous ground tissue. Phloems Nos. 1 and 2 come into direct contact with each other, surrounding a contiguous xylem. The fibre ring loses its sinuosity. At the same time, the central transporting bundle of the midrib becomes surrounded by the bundle sheath parenchyma instead of the parenchymatous ground tissue. There are octahedron crystals in the cell row of the bundle sheath parenchyma in contact with the fibre bundle sheath. In the midrib of the leaf blade, containing still dividing cells, these crystals are small; by autumn, on the other hand, they almost completely fill up the parenchymatous cells. The bundle sheath parenchyma around the midrib is of several rows of cells, its outer cells are in contact with the epidermis on the dorsal and ventral sides of the leaf. In the leaf blade the bundle sheath parenchyma is in contact with the mesophyll cells.

In the cross-section of the petiole, the cells of the phloem fibre ring are of an irregular polygonal form, elongated. The phloem contains sieve tubes, companion cells and phloem parenchymatous cells. In the xylem the tracheae lie dispersed, singly or in small groups, their cell walls spirally thickened. The tracheae are peritracheally surrounded by parenchymatous cells. The xylem contains fibre elements as well. The shape of the parenchymatous ground tissue cells, in contact with vascular bundle No. 1, is oval; the longitudinal

wall of these cells shows pitted thickening. The cells of the transporting bundle of the petiole continuing in the midrib of the leaf are the same in form as those in the petiole.

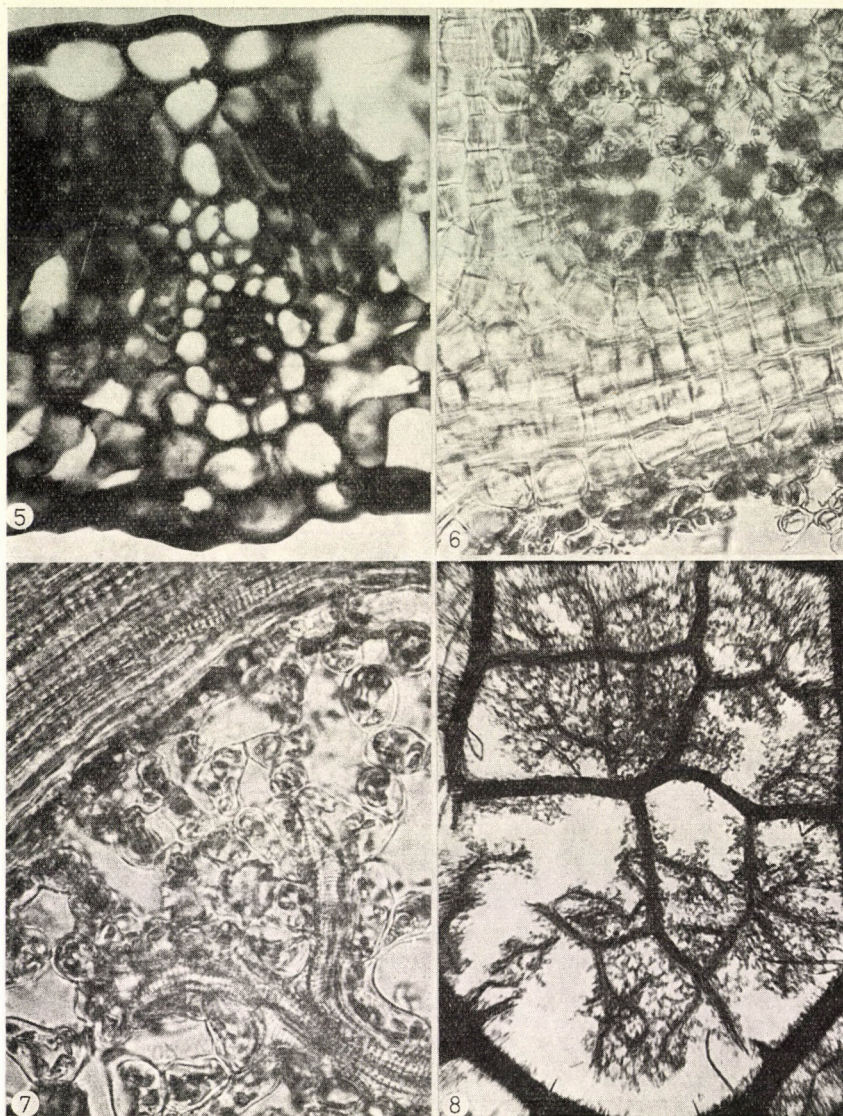
The branchings at the third and further orders in the transporting bundle start from the two parallel lateral veins at an angle of 90°, almost confronting each other; they meet and then by another ramification of opposite direction form rib islands in the leaf blade.

The lateral veins of the third and fourth order usually contain one transporting bundle, where the xylem is in the middle, the phloem on the dorsal and ventral sides — the latter with a small phloem fibre ring of a few rows of cells (Photo 4). The vascular bundle is surrounded by the bundle sheath parenchyma here too. Its special formation the bundle sheath extension, was distinguished by WYLIE (1951, 1952; Photo 5). Only these extension of the bundle sheath parenchyma of the tertiary but especially of the quaternary lateral veins reach the lower and upper epidermis. WYLIE attributes an important extravascular transporting role to these extensions, since their parenchymatous cells are in direct contact with the assimilating cells. ARMACOST (1944) showed that the parenchyma cells surrounding the transporting bundle system are especially permeable. WYLIE has already mentioned that in the case of several dicotyledonous plants the bundle sheath parenchymatous cells contain crystal. The same is valid for *Quercus pubescens*, wherever the parenchymatous extensions of the bundle sheath exist (Photo 6). We can rely only on hypotheses whether these crystals inhibit transporting or if their role is something else.

Concerning the small transporting bundle (= minor vein) endings in the mesophyll of the *Quercus pubescens*, the situation is different. These vein endings — which are found in the mesophyll of the leaf, in the layer between the palisade and spongy parenchymas — usually consist of only 1—2 tracheids surrounded by xylem parenchymatous cells of chloroplast content and showing a transitional form (Photo 7). For the transporting role of the latter, the hypothesis of WYLIE and ARMACOST is more acceptable.

By ultrastructural examinations, GUNNING and PATE (1970) have recently widened our information on the parenchyma cells of this type; they called them "transfer cells". They stated: "... two other types (C- and D cells) occur in xylem parenchyma and bundle sheath respectively, and have ingrowths only on walls in contact with or in close proximity to vessels or tracheids". And "On the basis of their location and of orientation of their wall ingrowths we have implicated C- and D-type cells in absorbing materials from xylem." (The A and B cell types, described by these authors, appear definitely bound to the phloem and xylem.)

Physiological studies, starting from the investigations by KORTSCHAK — HARTT—BURR (1965), called attention to the function producing organic

Plate II. 5. Leaf cross-section. In the middle a smaller transporting bundle with its parenchymatous cells of bundle sheath extension communicating with the epidermis cells. $\times$840. 6. Paradermal section of secondary and tertiary lateral veins. The parenchymatous cells are filled with crystals. $\times$510. 7. Termination of transporting bundle in the spongy parenchyma layer of the leaf. Tracheids with adjacent bundle sheath parenchymatous cells containing chloroplast. $\times$680. 8. Vein system of the leaf blade with mesophyll chambers and vein endings. $\times$ about 200

matter of the bundle sheath parenchymatous cells with chloroplast content.

So, in the *Quercus pubescens* leaf, the parenchymatous cells of ground tissue in the petiole, and partly also the same ground tissue in the midrib as well as the bundle sheath parenchymatous cells of the small transporting bundle endings, contain chloroplast. In contrast with this, there are crystals in the bundle sheath parenchyma cells of the secondary and tertiary lateral veins.

The parenchymatous cells of the minor vein endings — according to data in the literature — partly pass the dissolved salts, transported by the xylem, towards the assimilating cells of the mesophyll, but assumably they perform opposite and lateral transportation as well.

The leaf blade

Stomata are absent on the upper side of the leaf, while on its underside they are in abundance;* their number is increasing from the midrib towards the marginal part of the leaf. The hair basis cells of the hairs covering the surface of the whole leaf are inserted among the epidermis cells lying above the transporting bundle. The branched hairs are shorter on the upper side of the leaf, longer on the underside and on the petiole.

In the mesophyll of the leaf, the vein island surrounded by the transporting bundles is the mesophyll chamber (after WYLIE 1952), the side walls of which are constituted by the parenchymatous cells of bundle sheath, or their extensions, while the dorsal and ventral walls by the epidermis (Photo 8; Fig. 1). The decurrence of the bundle sheath extensions on the outer surface of the leaf epidermis (or on the proof of collodium) is well observable under the microscope, since the epidermis cells are elongate at their junction, no stoma occurs, or forms but rarely in their line (Photos 9 and 10). Within the mesophyll or the chambers, the palisade parenchymatous locally biseriate (Photo 11) in the leaves of individuals rich in light (grown in the third and fourth habitat types). If only one cell row develops, these cells are considerably elongated. Comparing the two habitat types of extreme light supply, in the middle of the mesophyll chamber 11 palisade parenchymatous cells are found under one epidermis cell in the leaves from the 4th habitat type, while 12—13 palisade parenchymatous cells, occur on the sides; in the leaves from the first habitat type there are, 8—10 and 9—12 of them; the palisade parenchyma is uniseriate in the latter (Photos 12, 13, 14). Palisade parenchymatous cells frequently lie under two adjacent epidermis cells.

*Concerning their formation, they are anysocytic = of the *Ranunculaceae* type, without subsidiary cells.

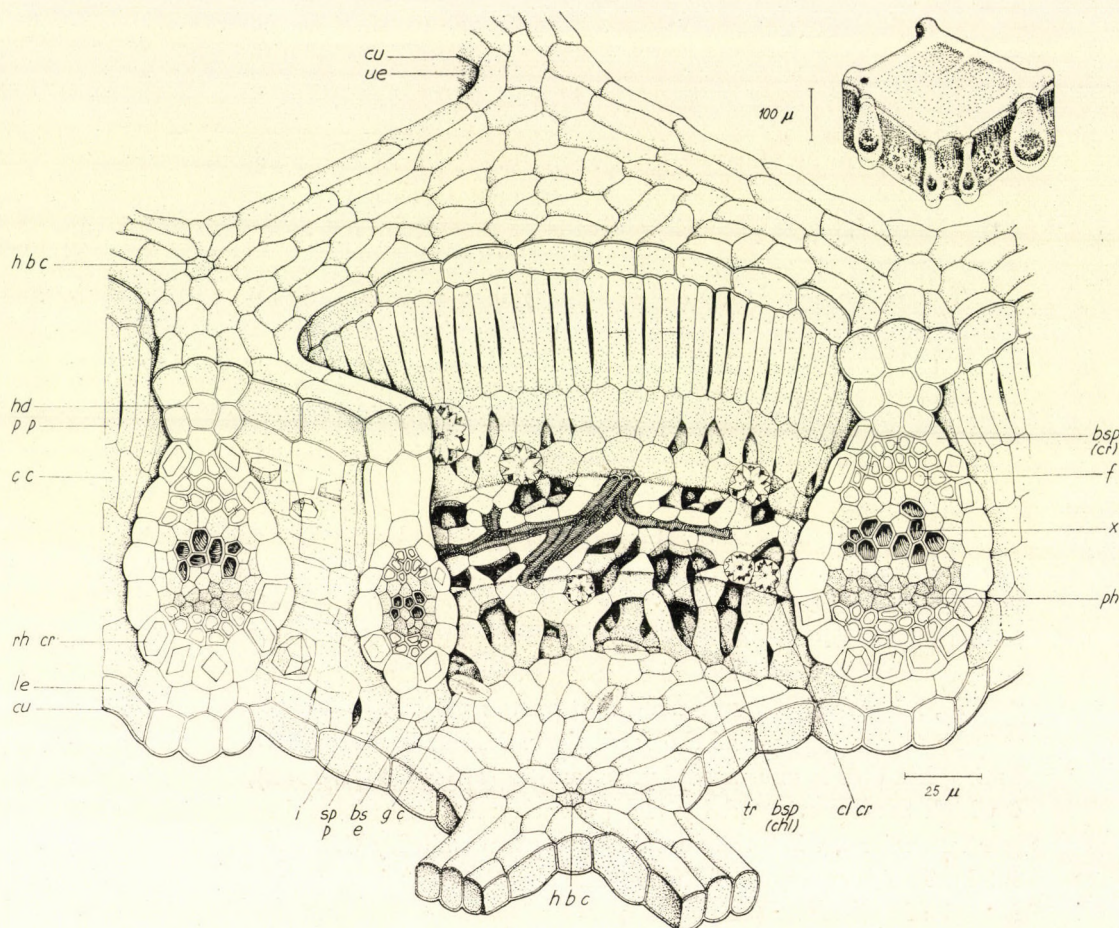



Fig. 1. Stereoscopic picture of a mesophyll chamber from the leaf of *Quercus pubescens*. Abbreviations (counter-clockwise): cu = cuticle, ue = upper epidermis, h b c = hair basis cell, hd = hypodermal cell, p p = palisade parenchyma, c c = collecting cell, rh cr = rhombic crystal, l e = lower epidermis, i = intercellular, s p = spongy parenchyma, b s e = bundle sheat extension, g c = guard cell, h b c = hair basis cell, tr = tracheide, b s p (chl) = bundle sheat parenchyma with chloroplast, cl cr = cluster (druse) crystal, ph = phloem, x = xylem, f = fibre, b s p (cr) bundle sheath parenchyma with crystal

The palisade parenchymatous cell rows are followed by the still slightly column-shaped cells of the transitional cell row. The dorsal tops of these cells are usually in contact with the basis of two palisade parenchymatous cells while their ventral top slightly widens (Photo 15). In paradermal sections it is well observable that the cells of the second (inner) row of cells in the spongy parenchyma are connected with the ventral top of the collecting cells, surrounding it as a centre. The meshed cell structure (after WYLIE 1951) is well observable in the paradermal sections (Photo 16).

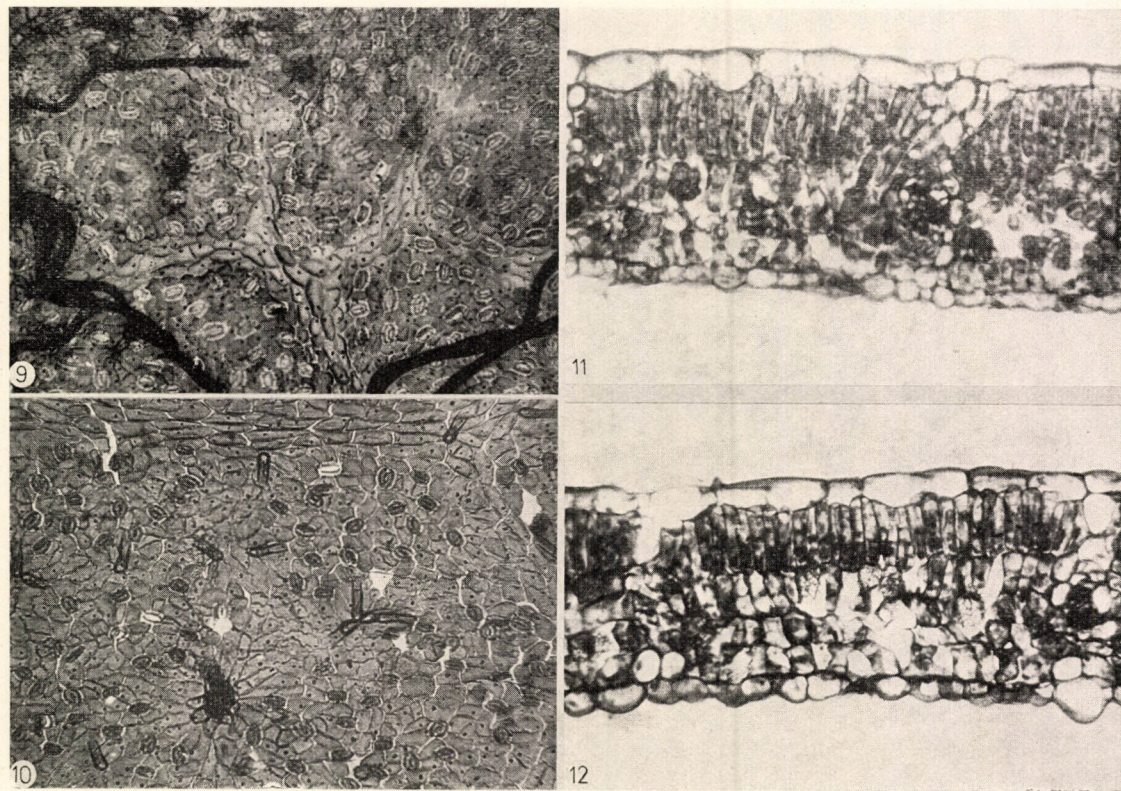



Plate III. 9. Underside epidermis from the 4th habitat type. With elongated epidermis cells above the transporting bundles, and with stomata in the intercostal fields. Small mesophyll chambers. ×150. 10. Leaf epidermis from the first habitat type. Large mesophyll chambers. ×150. 11. Leaf cross-section from the 4th habitat type, with elongated locally biseriate palisade parenchyma cells. ×360. 12. Leaf cross-section from the first habitat type. ×360

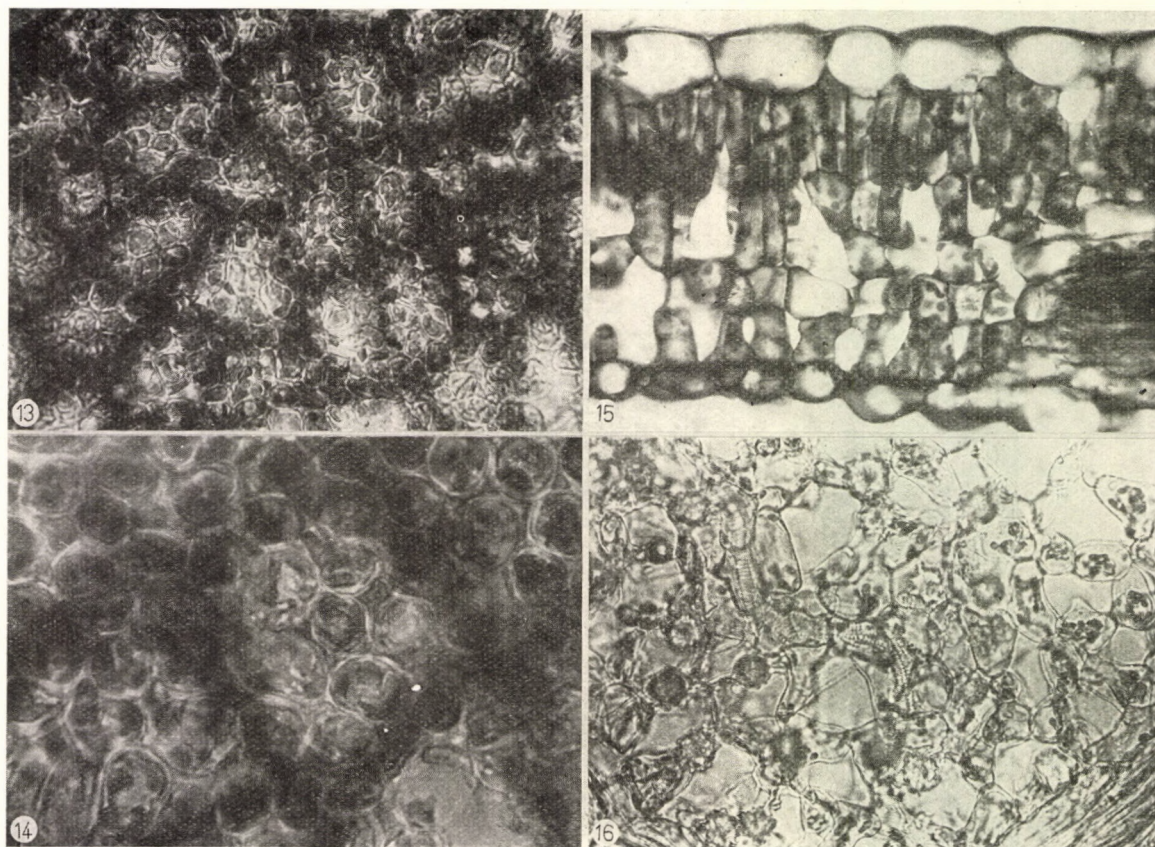



Plate IV. 13. Paradermal section from the dorsal part of a *Quercus pubescens* leat. The border of the epidermal cells appears in the form of a black mesh. Palisade parenchyma cells under the individual epidermal cells are distinguishable. ×550. 14. Palisade parenchyma cells, containing chloroplasts under the individual epidermal cells. ×1400. 15. Cross-section of leaf mesophyll. ×560. 16. Meshed cell structure of spongy parenchyma. The cells of the spongy parenchyma locally connected with the ventral top of the collecting cells. Plastids and crystals observable in the cells. ×550

At the endings of the minor veins parenchymatous cells containing chloroplast are found instead of the spongy parenchyma. These small minor vein endings are simple (not branching) in the leaves grown in habitat types poor in light; they form small dendrites in habitat types rich in light, further dividing the chambers (Photo 7).

It follows from the description above that the mesophyll chamber may be considered the organic matter production and transport unit of the leaf (and not only of the gas supply; cf. WYLIE 1952). The number of chambers per unit of leaf area and within these the number of minor vein endings may be a factor determining the transport capacity. The transport of water, and of ions dissolved in it, takes place also within the chambers.

Cell content. Palisade and spongy parenchymatous cells as well as parenchymatous cells surrounding the small vein endings have a chloroplast content, although the number of these plastids is different. (In the case of other plant species, also structural deviations were recognized in the plastids of parenchymatous cells surrounding the transporting bundle.) In the palisade parenchymatous cells, the arrangement of the plastids depends on light (RABINOWITCH 1951, and many others), while in the spongy parenchymatous cells the plastids gather in the tops of the arms (Photos 14 and 16).

The nucleus in usually in the middle of the cell. As has been mentioned above, the bundle sheath parenchymatous cells surrounding the larger transporting bundles contain octahedrous, bipyramidal etc. crystals.

Other cell inclusions. Enormous lithocysts can be found between the palisade parenchymatous cells, with large druse crystals in them beside the cytoplasm. The druse crystals occurring in the second row of cells in the spongy parenchyma are of smaller size but more frequent. Their number and size grows with the age of the leaf (Photos 12 and 15).

Intercellulars. The size, form and number of intercellulars depend partly on the form of cells bringing them into existence, partly on their arrangement in the mesophyll. It is well observable in paradermal transsections that the intercellulars can take a considerable volume even between palisade parenchymatous cells. It is also conspicuous in such transsections that the intercellulars of the second row of cells in the spongy parenchyma assume a larger volume than those in the first row. By the sides of the larger transporting bundles, the cells of the mesophyll are not closely aligned: the intercellulars found here are large and of irregular form.

On the ventral side of the leaf, the inner chamber of the stomata is mostly in contact with the intercellulars between the cells of the first cell row of the spongy parenchyma. Within a mesophyll chamber the intercellulars are in a labirynthine connection with one another (Figs 1, 2 and 3).

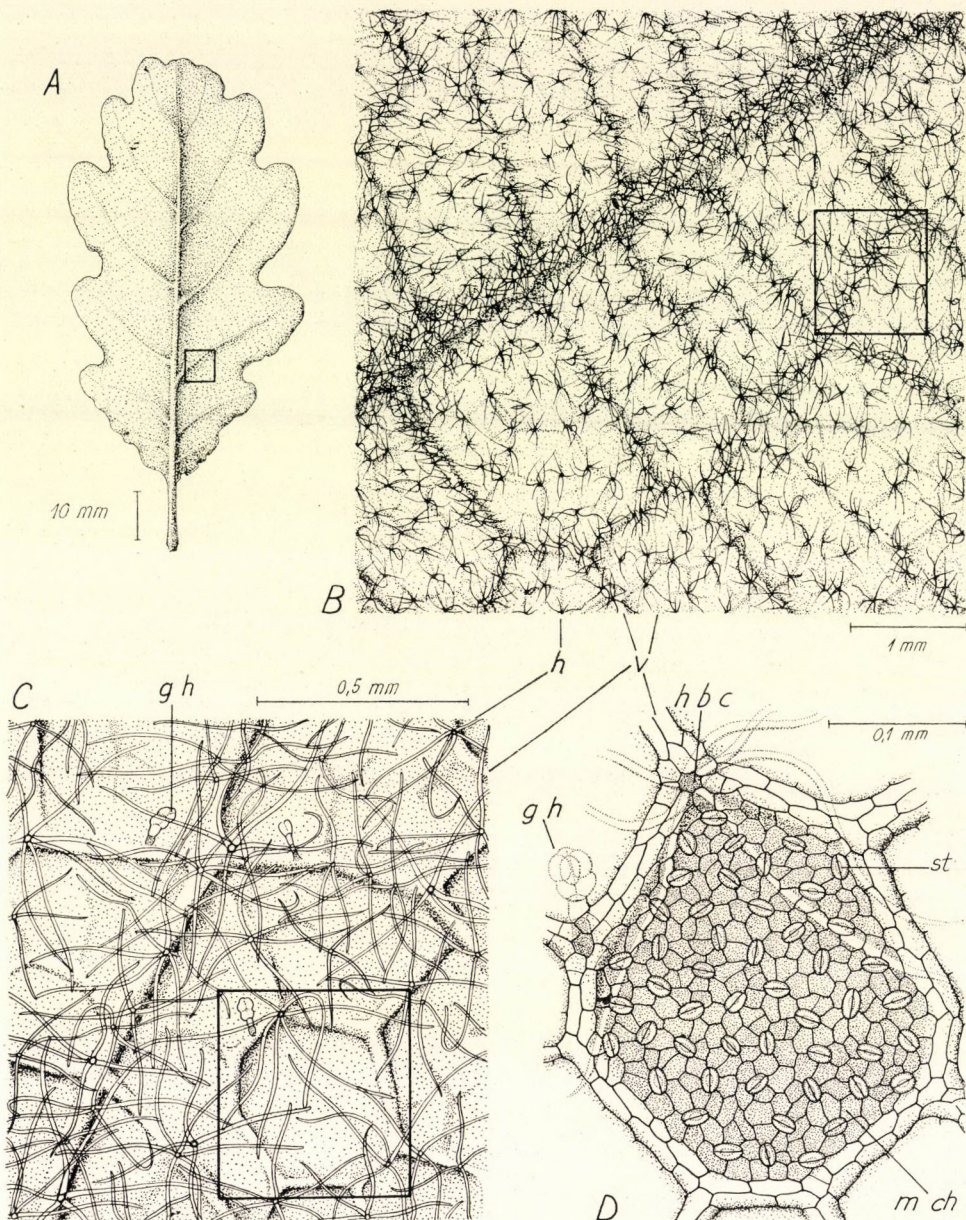



Fig. 2. Quercus pubescens leaf (A); part of underside of the leaf with ribs surrounding mesophyll chambers and with hairs (B); stellate hairs and secretory gland situated above the transporting bundles (C); mesophyll chambers with stomata (D); Abbreviations: g h = glandular hair, h = hair, v = veins (subjacent with bundle sheath parenchyma), h b c = hair basis cell, st = stoma, m ch = mesophyll chamber

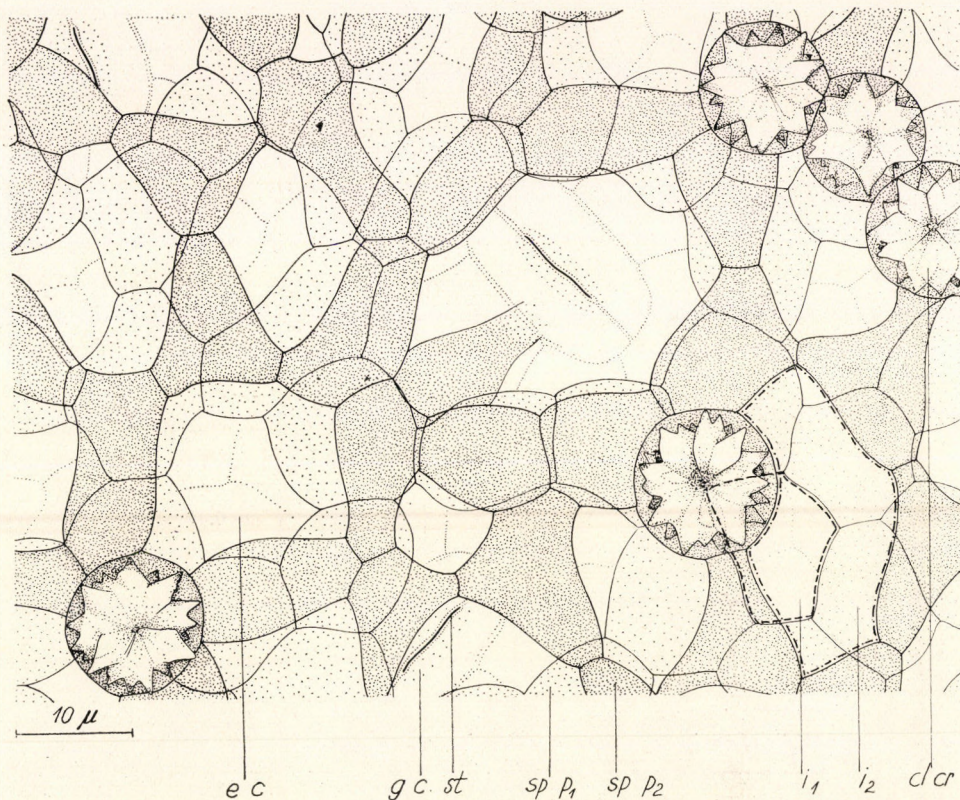



Fig. 3. Position of intercellulars and their differences in dimension in two layers of spongy parenchyma. Abbreviations: e c = epidermal cell, g c = guard cell, st = stoma, sp p_1 = = spongy parenchyma, 1st (outer) layer, sp p_2 = spongy parenchyma, 2nd (inner) layer, i_1 = intercellular space in the 1st (outer) spongy parenchyma layer, i_2 = intercellular space in the 2nd (inner) spongy parenchyma layer, cl cr = cluster (druse) crystal

Results of the quantitative leaf anatomical investigations

Prior to the leaf anatomical investigations as such, and for gathering information, the fresh weight for 1 cm^2 of leaf was calculated. According to McClendon (1962), this value — the density thickness — gives a good approximation of the leaf thickness.

In Table 9, the separation of the values according to light (the effect of the first two habitat types in contrast with that of the third ad fourth) appears distinctly.

The differences appearing in the leaf thickness are attributable to the palisade parenchyma, since the proportion of this layer to the whole mesophyll shows the same tendency (Photos 11 and 12; Fig. 4/b).

Table 9

Density thickness of the leaves of the sample trees investigated (mg fresh weight per sq. cm)

Habitat type	1	2	3	Average
1	12.4	13.7	14.3	13.47
2	12.2	12.8	16.2	13.73
3	15.9	13.8	16.4	15.37
4	17.4	15.4	14.9	15.90

Table 10

Data of the palisade parenchyma per mesophyll rate

Habitat type	1	2	3	Average
1	0.46	0.40	0.37	0.410
2	0.31	0.50	0.51	0.440
3	0.56	0.56	0.57	0.563
4	0.54	0.53	0.57	0.546

Table 11

Analysis of variance of the data of palisade parenchyma per mesophyll rate

Source of variability	SQ	df	MS
Total	0.0860	11	—
Factor combinations	0.0520	3	0.0173*
Factor A	0.0500	1	0.0500**
Factor B	0.0001	1	0.0001
A×B interaction	0.0019	1	0.0019
Error	0.0340	8	0.0042

Table 12

Averages, differences and significance levels in the data of the palisade parenchyma per mesophyll rate according to habitat types

Habitat type	1	2	3	4
1	0.410	0.030	0.153	0.136
2		0.440	0.123	0.106
3	X	X	0.563	0.017
4	X			0.546

As can be seen from the tables, the highest values are encountered in the third habitat type (the "most favourable" concerning light and water supply); the values are higher here than in the fourth habitat type and the two differences obtained in the comparison per pairs refer also to the third habitat type.

If the palisade parenchyma rate is related merely to the spongy parenchyma (projection-planimetric method), then the separation of the characteristic investigated according to habitat types is rather conspicuous.

Table 13

Data of palisade per spongy parenchyma rate

Habitat type	1	2	3	Average
1	1.41	1.11	1.03	1.183
2	1.00	0.86	0.74	0.866
3	2.01	1.79	1.83	1.877
4	1.85	1.95	2.34	2.046

Table 14

Analysis of variance of the data

Source of variability	SQ	df	MS
Total	3.1015	11	—
Factor combinations	2.8258	3	0.9419***
Factor A	2.6320	1	2.6320***
Factor B	0.0161	1	0.0161
A×B interaction	0.1777	1	0.1777
Error	0.2757	8	0.0344

Table 15

Averages, differences and significance levels in the data of the palisade per spongy parenchyma rate according to habitat types

Habitat type	1	2	3	4
1	1.183	0.317	0.694	0.863
2		0.866	1.011	1.180
3	XX	XXX	1.877	0.169
4	XXX	XXX		2.046

At the rate of mesophyll layer measured in the above way, the influence of the fourth habitat type is sharply outstanding.

In breaking down to factors, the light factor alone is of significant influence on the development of the palisade parenchyma layer (Tables 11 and 14).

Since the sample was taken from the shade leaves of the lowest branch of each tree, also the shade leaves of the third and fourth habitat types can be regarded as sun leaves in comparison with the leaves examined from the sample trees of the first and second habitat types. The anatomical differences in the mesophylls of leaves from the sample trees grown in the two extreme habitat types have already been discussed in the preceding chapter.

The size of the mesophyll chambers (Fig. 1) differs considerably according to habitat types; it is monotonously decreasing from the habitat types with low light intensity and good water economy to those of good light supply and bad water economy (Photos 9 and 10; Fig. 4/a).

When breaking down to factors, the light factor and the water factor are of significant influence also separately.

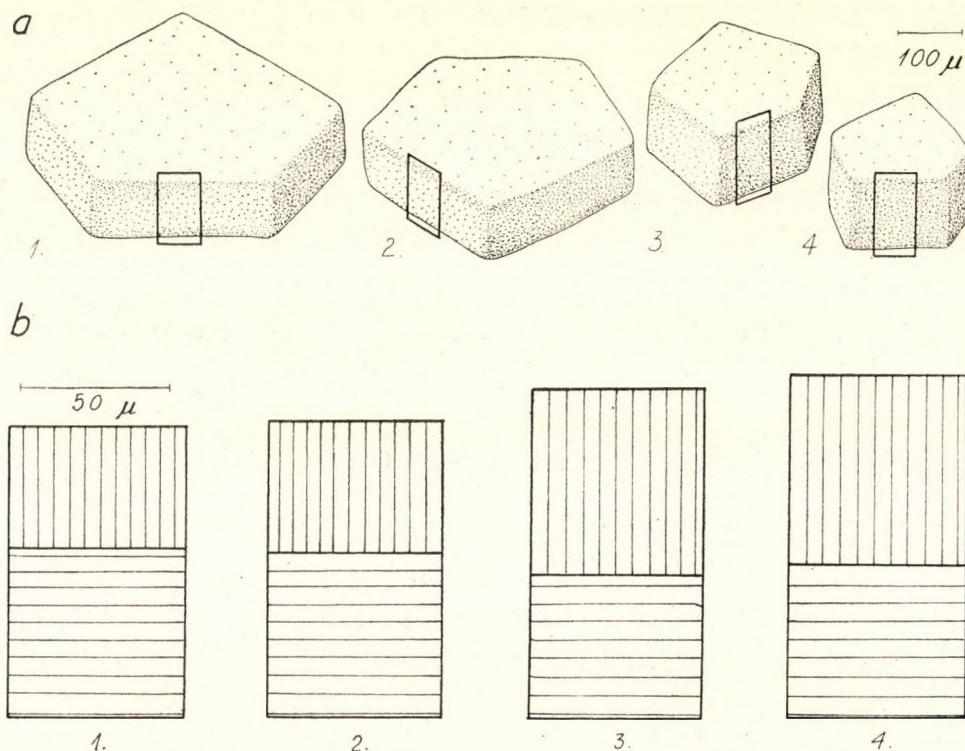



Fig. 4. Volume change in the mesophyll chamber, according to habitat types, in outlines (a). Change in the proportion of palisade per spongy parenchyma, according to habitat types, in outlines (b)

Table 16

Volume data of the mesophyll chambers
(in 10^6 μ^3)

Habitat type	1	2	3	Average
1	14.75	14.14	13.38	14.090
2	14.94	9.37	10.98	11.763
3	5.39	9.88	8.06	7.777
4	4.79	3.92	5.71	4.807

Table 17

Analysis of variance of the data of mesophyll chambers

Source of variability	SQ	df	MS
Total	182.658	11	—
Factor combinations	153.462	3	51.154**
Factor A	131.000	1	131.000***
Factor B	21.000	1	21.000*
A×B interaction	1.462	1	1.462
Error	29.196	8	3.649

Table 18

Averages, differences and levels of significance of the sizes of mesophyll chambers according to habitat types

Habitat type	1	2	3	4
1	14.090	2.327	6.313	9.283
2		11.763	3.986	6.956
3	XX	X	7.777	2.970
4	XXX	XX		4.807

With regard to the development of intercellulars, the picture is different. The intercellulars of the leaves from trees grown in the fourth habitat type are of a stronger development than those in the first three habitat types. Microscopic photographs also show that the layer of collecting cells in the fourth habitat type breaks up and great intercellular cavities arise among it and the neighbouring spongy parenchymatous cells. Locally, narrow intercellulars are wedged in also between the palisade parenchymatous cells. The mesophyll of the leaves in habitat types 1 and 2 does not show on the other

hand, the disintegrating structure experienced in the shade leaves of shade-enduring species (e.g. *Fagus silvatica*; cf. SÁRKÁNY and SZALAI 1957; Photos 11 and 12).

Table 19 shows the area proportion of intercellulars related to the mesophyll layers (layers of palisade parenchyma + spongy parenchyma + collecting cells).

The statistically demonstrated, outstanding intercellular rate in the leaves of the sample trees in the fourth habitat type is shown also in a comparison according to pairs, while in habitat types 1—3 the values are more conforming.

Table 19

Relative area proportion of intercellulars (intercellular-rate)

Habitat type	1	2	3	Average
1	0.08	0.08	0.08	0.080
2	0.09	0.12	0.07	0.093
3	0.08	0.05	0.10	0.077
4	0.14	0.13	0.13	0.133

Table 20

Analysis of variance of the data

Source of variability	SQ	df	MS
Total	0.0087	11	—
Factor combinations	0.0061	3	0.0020*
Factor A	0.0010	1	0.0010
Factor B	0.0037	1	0.0037**
A×B interaction	0.0014	1	0.0014
Error	0.0026	8	0.00032

Table 21

Averages, their differences and levels of significance of the data of the intercellular rate, according to habitat types

Habitat type	1	2	3	4
1	0.080	0.013	0.003	0.053
2		0.093	0.016	0.040
3			0.077	0.056
4	XX	X	XX	0.133

The breaking down to factors shows that the influence of the light factor on the intercellular rate is no more significant, while that of the water factor is still significant.

Stoma frequencies, as can be seen in Table 22 are higher in individuals growing in the second and fourth habitat types ("little water" habitattypes). They are lower in the first and third habitat types with good water supply. The influence of the fourth habitat type is the strongest also on stoma frequency. A breakdown to factors revealed also here that the water factor in itself is effective.

Table 22

The data of stoma numbers for 1 sq. mm (values to be multiplied by 10^2)

Habitat type	1	2	3	Average
1	4.47	4.43	2.92	3.940
2	4.70	4.68	4.86	4.746
3	3.82	3.55	3.32	3.563
4	5.15	5.98	6.00	5.710

Table 23

Analysis of variance of the data

Source of variability	SQ	df	MS
Total	10.323	11	—
Factor combinations	8.147	3	2.715**
Factor A	0.259	1	0.259
Factor B	6.543	1	6.543**
A×B interaction	1.345	1	1.345
Error	2.176	8	0.272

Table 24

Stoma number averages, their differences and levels of significance according to habitat types

Habitat type	1	2	3	4
1	3.940	0.806	0.377	1.770
2		4.746	1.183	0.964
3		X	3.563	2.147
4	XX		XX	5.710

Discussion

Assessing the results, it may be stated that the palisade per spongy parenchyma (or palisade per mesophyll) rate in a comparison according to pairs of habitat types shows difference only where opposite light levels are collated. In a comparison with other leaf anatomical characteristics, the difference arose also in these four cases between the averages of mesophyll chamber sizes according to habitat types. Thus, even within identical water supply levels, these differences arise for both characteristics habitat type pairs (1—3 and 2—4). The identical affection by the habitat types of these two leaf anatomical characteristics, as well as the strong (at 1% level) correlation between the rate of the assimilating layers and the dimensions of the mesophyll chamber (Table 25) may suggest a connection possibly existing in their evolvement.

There is abundant literature in the stronger development of the palisade parenchyma on the effect of a higher intensity or longer duration of light i.e. on the inducing role of light. STAHL demonstrated already in 1880 (and 1883), on species growing in habitat types rich in light, that on both the dorsal and the ventral sides of bifacial leaves a palisade parenchyma of several cell rows can form. This was investigated by SCHNEIDER (1952) in *Ficus elastica*. Under artificial conditions, TURRELL (1944) and since then several authors have been able to demonstrate a change in rate in the two parenchymatous layers, even in the case of identical species, by a preliminary growth in low and high light intensities. On the effect of light on the development of mesophyll layers see also THODAY 1931, WATSON 1942; summarizing literatures by SHIELDS up to 1950; by STARZECKI up to 1962; ESAU (1969), etc. On the other hand, it was only TURRELL (1944) who dealt with the mathematical-statistical evaluation. Our data concerning *Quercus pubescens* corroborate now also statistically

Table 25

Values of the correlation coefficient among the anatomical characteristics investigated

	r
Rate of palisade parenchyma per mesophyll — volume of mesophyll chambers	−0.778**
Rate of palisade parenchyma per mesophyll — intercellular rate	0.270
Rate of palisade parenchyma per mesophyll — stoma number	0.201
Rate of palisade per spongy parenchyma — volume of mesophyll chambers	−0.742**
Rate of palisade per spongy parenchyma — intercellular rate	0.375
Rate of palisade per spongy parenchyma — stoma number	0.252
Mesophyll chambers size — intercellular rate	−0.627*
Size of mesophyll chambers — stoma number	−0.412
Intercellular rate — stoma number	0.670

the effect of the intensity and the duration of light, independent of water supply on the evolvement of the rates of the assimilating layers.

The rate of the assimilating layers of the mesophyll and the size of the mesophyll chambers, respectively, may be induced at in on early phase of the leaf growth. For example, TETLEY (1932) observed that in the growth of plum leaf-buds the epidermal cells elongate, the leaf spreads and then the mesophyll cells continuously divide. ISONOGLE's (1944) investigations on deciduous trees suggest that varying light, as an ecological effect, induces the various sizes of mesophyll layers during the bud and young leaf state. This assumption seems to hold also of *Quercus pubescens*, since the values of the spring light intensity run other correspondingly to the growth of the palisade parenchyma (see Tables 6 and 15).

Data on the relationship between the assimilating layers of the mesophyll and the distance of the adjacent bundle sheath extensions (that is on its two-dimensional measure) are given by WYLIE (1951). He examined ten tree species, sun leaves and grades of shade leaves in each. The higher palisade per spongy parenchyma rate of the sun leaves decreased towards the shade leaves, while the distance between the bundle sheath extensions increased. This relationship has now been demonstrated concerning the mesophyll chambers (in three dimensions) in *Quercus pubescens*, in various individuals ($P = 1\%$). According to our investigations, light and water supply may be responsible, and also separately, for the variability in the size of the chambers.

The possibility of the mesophyll chamber being a unit of gas supply was suggested also by WYLIE (1952). The fact that in *Quercus pubescens* the relative area of the intercellulars increases with the decrease in chamber size (for the connection at 5% probability level see Table 25) may contribute to the approach concerning the possible role played by the chambers in the control of gas supply.

The analysis of the intercellular rate furnished surprising results, as this rate is the highest in the fourth habitat type, where is associates with the most xeromorphous leaf characteristics. TURRELL pointed out already in 1936 that the relative exposed surface is greater in xeromorphous sun leaves than in shade leaves; however, we do not know to what extent the results obtained by our measurement methods allows a comparison with the measurements related to the exposed cell surfaces. The coming into existence of the intercellulars in the fourth habitat type of *Quercus pubescens* may partly be caused by the considerable elongation perpendicular to the leaf surface of the palisade parenchymatous cells; this is associated to a more considerable extent with the producing of intercellular cavities along the anticlinal cell walls than in the other habitat types.* Anyhow, following from this higher intercellular

* A further cause of differences in the intercellular sizes according to habitat types may be the number of differing palisade parenchymatous cells per unit leaf area.

rate, a more powerful gas-capacity may be expected, as also suggested by communications in the literature (for example, the porometer experiments by NIUS, 1931).

As has been mentioned, the intercellulars are contiguous within the mesophyll chamber. WILLIAMS (1948) established by the help of a porometer that in the leaf of *Pelargonium* air diffuses even through the parenchymatous cells separating the mesophyll chambers. From this he inferred that the oxygen or CO_2 of the atmosphere can diffuse laterally through the leaf even if the whole system of the intercellulars is not contiguous in the mesophyll (as for example in the leaf of *Quercus pubescens*).

The physiological role of the intercellulars, their connection with the active surface of the cells surrounding them, and besides this with the stomatal function, lies in a partly discovered and a partly still unknown relationship. The intercellulars are in contact with an enormous inner cell surface considerably larger than the outer surface; their quotient is TURRELL's "relative exposed surface"; (TURRELL 1936, 1944). At the same time, these cell surfaces are covered in certain species with a thin cutin layer (according to FREY-WYSSLING and HÄUSERMANN 1941). Therefore, already also on account of this, they have their own resistance against CO_2 assimilation (mesophyll resistance). In the opinion of WYLIE (1947), this cutin layer does not play a considerable regulatory role in transpiration, i.e. the diffusion of water from the cells towards the intercellulars. This is why TURRELL's (1944) leaves had, possessing artificially induced high inner exposed surfaces, a high transpiration capacity. The positive correlation, significant at 2%, of the intercellulars with the stoma number may also indicate the intercellulars' role related to gas supply in *Quercus pubescens* (Table 25). The spatial relationship between intercellulars and stomata was discussed in the anatomical description.

When estimating the ecological role of stomata, the question may arise whether it is more appropriate to work with stoma numbers related to unit area, or with stoma indices? The later (cf. SALISBURY 1928, 1932; PONT 1939) or the stoma number per epidermical cell number (SCHÜRMANN 1959) are also suitable for ecological use; they express and record mainly the water and light supply conditions of the plant at the time of differentiation of stomata. The advantage of these indices is that they filter the differences originating from the deviations in insertion, the nodal situation, and the growth of the leaf by establishing a standard related to the epidermis cell number. This advantage could, however be dispensed with (see the chapter on sampling). The stoma per epidermical cell number reacts to the water supply relations with an opposite trend to stoma frequency (according to SCHÜRMANN, the epidermical cells are produced in a relatively greater number than the stomatal primordia in drier habitat types — in contrast to the situation in the control plants — though the number of the stomatal primordia is also greater per the area unit than

in the control plant with a good water supply). Since bad water and good light supply is of an antagonistic influence on the value of the quotient mentioned above, it would probably blur the differences in the system investigated. Presumably, it were more reasonable if in our case the stoma supply for surface unit with regard to metabolism physiology, (the CO_2 supply of the mesophyll) would be given in absolute figures and independently of the number of epidermical cells.

In *Quercus pubescens*, the stoma number is rather independent of leaf size; within identical treatment the stoma number does not follow in general the fluctuations in leaf size (a similar statement was made for tomato by FARKAS and RAJHÁTHY 1955).

As to the cause of low or high stoma frequency, the various research workers are not in agreement. Considering one of the essential functions of stomata, the rate of their frequency may be related to the water factor. SALISBURY's (1928) experiments with *Scilla nutans*, NIEMANN's works (1932) as well as SCHÜRMANN's investigations (1. c) in cultivated plants indicate a strong stomatal induction by water supply. By rendering water supply difficult, SCHRÖDER (1938) induced in *Fagus silvatica* high stoma frequency even among shade leaves with low stoma numbers; recently, for example, GINDEL (1969) demonstrated experimentally that with the reduction in soil humidity a higher stoma density evolves. On the other hand, the effect of light intensity on stoma density is emphasized by DODILLET (1956); the role of the duration of light by GÜMMER (1949).

Our investigations with *Quercus pubescens* established the significant influence of soil water supply on the density of stomata. The effect of the water supply (and through this also of other factors) in the soil can be conceived as a process, by the intakeable water regulating the water metabolism of the leaf (influence on the hydrature — the production of a deficit in water saturation — and enzyme activity; cf. FARKAS and RAJHÁTHY 1. c., etc.), and through this the epidermis system (promotion or inhibition of epidermical cell division, stimulation or inhibition of new stomatal primordia coming into existence; activation or inactivation of the stomatal inhibition zone; SCHÜRMANN 1. c., etc.).

On the basis of their higher stoma frequency, the leaves of trees grown in the second and fourth habitat types can presumably transpire more strongly. This assumption is substantiated the relation demonstrated between the stoma number and the intercellular rate. There are also many references in the literature to the stronger transpiration ability of leaves with great stoma number (cf. GRIGORJEV 1955; recently e.g. JANKE, 1970, pointed out experimentally that the transpiration resistance of *Vaccinium myrtillus* is inversely proportional with the stoma number; cf. in this respect also KNIGHT, 1965). As for *Quercus pubescens*, experimental proof is necessary. Besides, important factors in transpiration are the openness of stomata (see HEATH, MEIDNER 1960),

the rhythm of opening-closing, and the degrees of openness and its duration.

Evaluating the development and relation of the examined four leaf anatomical characteristics as a function of the same ecological factors it can be stated that in the mesophyll the rate of the assimilating layers (palisade per spongy parenchyma and palisade per mesophyll rates) show a relationship only with the size of the mesophyll chambers. On the other hand, the size of the mesophyll chambers is correlated with the intercellular rate. Only this latter characteristic can statistically be brought into relationship with the examined quantitative characteristic of the epidermis: with the stoma number; hence the intercellulars establish a connection also in this quantitative sense between the mesophyll and the epidermis.

When considering which ecological factors has in itself an influence on the formation of the investigated four anatomical characteristics, the picture is as follows (as a result of summing up the breaking down to factors of the performed analyses of variance):

Table 26

Influence of the two ecological factors on the anatomical characteristics, with the usual designation of the significance levels

Anatomical characteristics	Light	Water
Rate of palisade per spongy parenchyma	XXX	
Size of mesophyll chamber	XXX	X
Intercellular rate		XX
Stoma number		XX

Therefore it is only light that influences the rate of assimilating layers in the mesophyll; the size of the mesophyll chamber is influenced by both factors. For the characteristics referring to the gaseous exchange (intercellular rate, stoma number), the influence of water is exclusive.

By testing the influence of factor combinations with the functional anatomical data, comparisons concerning the habitat types of *Quercus pubescens* can also be made.

Table 27 shows the frequency of statistically reliable differences between the habitat types, calculated by comparing per pair the average values (cf. Tables 15, 18, 21 and 24) of the four anatomical characteristics in the leaves of the sample trees.

As can be seen, there is significant difference in all the measured characteristics between the first and the fourth habitat types representing the two extremes in light and water supply (the habitat type of the two communities showing the greatest difference in the production of organic substance). Bet-

Table 27

Frequency of the statistically significant differences between the averages of the four leaf anatomical characteristics, per pair of habitat types. Designation of anatomical characteristics: I = palisade per spongy parenchyma rate, II = mesophyll chamber size, III = intercellular rate, IV = stoma frequency

Pair of habitat types	Anatomical characteristics showing differences	Frequency of differences
1–2	—	0
1–3	I, II	2
1–4	I, II, III, IV	4
2–3	I, II, IV	3
2–4	I, II, III	3
3–4	III, IV	2

ween the second and the third habitat types, counterposed also as regards the levels of the both factors, it is only the intercellular rate wherein on difference exists. The main cause of differences between the leaves of trees grown in habitat types of identical water supply is in the rate of the palisade per spongy parenchymas and in the size of the mesophyll chambers; these two characteristics show significant differences in dimension at the low and high levels of water supply, i.e. according to the opposing light levels.

The combination of the higher light level with the levels of water supply was more often the cause of a difference than the combinations of the low light level (16 : 12). However, the cause of this was that within the high light level, between the third and fourth habitat types, differences occurred in two cases (intercellular rate and stoma number), whereas within the low light intensity, between the first and the second habitat types, no difference occurred in any of the characteristics. This can be put also in another way; as regards the chosen two levels of light at the lower level the examined leaf anatomical characteristics are less responsive to the effect of a varying water supply than at the higher level.

It is also important that between the third and fourth habitat types (a high light intensity in both, but a differing water supply) there is a sudden change, a difference already in the characteristics referring to the gaseous exchange (intercellular rate, stoma frequency).

High light intensity combined with a low level of water supply (fourth habitat type) produce most of the extreme values in the anatomical characteristics, and are mostly (in 9 cases) the cause of differences (Table 27). The factor combination a_2b_2, besides (on owing to?) its anatomical consequences, has a strong influence upon the growth and physiognomy of *Quercus pubescens*. Between the third and fourth habitat types there is a community border and assumably also an ecosystem border.

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EXAMINATION OF THE TOXIC EFFECT OF COPPER SALTS IN MAIZE

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Very weak solutions blue vitriol and other copper salts stimulate photosynthesis, but after some time toxic symptoms appear on the leaf treated with them. According to our investigations, toxicosis or a "laesio" visible to the naked eye, is referable in these cases not to copper, but to the effect of vitriolic acid arising treatments with blue vitriol. What is new in this statement is the fact that the lesion is of a greater extent than vitriolic acid originating from the hydrolysis of blue vitriol can cause in the given very weak concentration.

The phenomenon can be explained by the fact that — owing to the selective ion uptake and the ion exchange accompanying it—additional H_2SO_4 quantities continually arise and their aggressive effect reaches a degree where lesion is a consequence.

Introduction

In our previous study the effect of copper ions on the gas production by photosynthesis was examined (FRENYÓ and NINH 1970) and the conclusion by KATOH and TAKAMIYA (1961) and by others that copper stimulates the process of photosynthesis was confirmed by recent data. At the same time it was also stated that copper is of toxic effect as well (FRENYÓ and MÁRTON 1958; TÖLGYESI 1969). This is why it is used in sprays and caustics (UBRIZSY 1965). — In the present study this actual — or apparent — contradiction is to be clarified, namely, what is the cause of copper vitriol of such concentration as is otherwise favourable for photosynthesis becoming toxic.

Material and method

Experiments were carried out on the leaves of young maize plants grown in greenhouse. The leaves were cut and their pieces of about 10 cm in length were merged into copper solutions of various concentrations for a period of usually not longer than a quarter of an hour, which still did not cause any considerable disturbance in the respiration of cells. Tap water was used in the case of the controls. In order to promote permeability "Sandovit" an agglutinative agent, was dripped in each merging solution.

After soaking, the leaf pieces were washed with tap water, then stored in vapourized atmosphere in Petri dishes for several hours so that expected symptoms could appear. Finally, in order to fix the toxic patches that developed, the leaves were dried by pressing between filter papers.

The preliminary experiments were carried out with copper vitriol solutions of 0.1 and 0.01 per cent concentrations (see photograph). In the successive experiments the 10 and 1 millequivalent (0.01 and 0.001 normal) solutions of the following copper (II) salts were used:

sulphate, chlorid, acetate, basic carbonate. Besides these, also the effect of acids was controlled. Finally, the pH-values of aqueous solutions prepared from the leaves previously treated with copper salt solutions, then washed and dried, were compared with the control values.

Discussion and conclusion

As a result of the experiments, the following order of toxicity could be established on the basis of spread in the necrotic patches that developed on the leaves: chlorid, sulphate acetate carbonate. The patches developing on

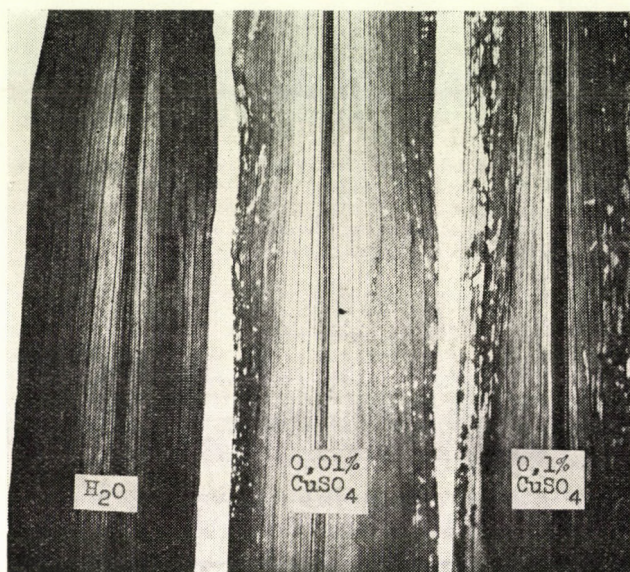
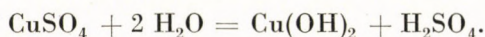



Fig. 1. Lesion on maize leaf, owing to the effect of copper sulphate solution of various concentrations. No damage on the control (H_2O); 0.01 per cent of copper sulphate caused visible damage; the effect of more concentrated solution (0.1 per cent) is proportionally stronger. Lesions were due to the decomposition of chlorophyll

the toxicated leaf were primarily caused by the decomposition of chlorophyll. This can be seen in Fig. 1.

The order of toxicity suggests that the salts of copper composing with strong acids cause a "laesion" to a greater extent than those with weak acids. This is not surprising because, the solution of copper vitriol, for example, hydrolizis according to the following equation:

$$CuSO_4 + 2\,H_2O = Cu(OH)_2 + H_2SO_4.$$

Free vitriolic acid emerges and it, naturally, attacks the chlorophyll in the cells, which gives rise to phaeophytine. It is, however, surprising that the

damage arising on the leaf is greater than what can be caused by the concentration of the acid escaping by hydrolysis. For living maize leaves merged into H_2SO_4 solution with a pH-value equivalent to a 0.01 per cent $CuSO_4$ solution were damaged less considerably than those merged into solution mentioned the above copper vitriol. In such a small concentration even Cu^{++} itself cannot cause toxosis, which is confirmed on the one hand by the fact that the fairly more concentrated bordeaux mixture is harmless and on the other hand by the inference that the weaker is the acid with which the copper composes into salt the less is the extent of laesion caused in the leaf. So, in the given concentration, neither the one, nor the other constituent is so toxic that it could give explanation for the extent of the lesion. Further, it is not assumable that the effects of cation and of anion add up, giving rise to synergism between the two opposing components.

The problem was brought nearer to solution by an experiment in which, besides the living leaves, also leaves devitalized by heat were used. When the leaves of young maize are merged in water at a temperature of 100°C for one minute the enzymes are destroyed but the chlorophyll remains intact. Since semipermeability ceases, the ions of the copper vitriol solution penetrate the inside of the devitalized cells by simple diffusion and, depending on the pH value of the solution, produce phaeophytine from the chlorophyll. This process takes place also in living leaves if "Sandovit", promoting the permeability of the leaf, is also present in the copper vitriol solution. However, after a few hours, usually more and extended patches arise in the living leaves than in the devitalized ones.

Assumably, the living cells — in a selective way — have taken in more Cu^{++} ions than SO_4^{--} ions. In such cases, the ions originating from the respiration of cells can at any time prevent the shift in the balance of charges, according to the following simplified equation: $CO_2 + H_2O \rightarrow H^+ + HCO_3^-$. During cation exchange, sulphuric acid "in statu nascendi" is arising up to the time when the cell takes up copper from the solution and, in place, discharges H^+ ion into the surroundings. The excess of sulphuric acid arising continuously in this way causes a more extended laesion on the leaf than the original acidity of the copper vitriol solution.

On our part, therefore, we attribute the toxic effect of copper vitriol and of other copper salts mainly to the acids arising "in statu nascendi" during the ion exchange.

Summary

Copper ions stimulate photosynthesis, but even a fairly weak solution of copper vitriol causes laesions in the leaf. On the strength of our investigations, the laesion can be attributed not to the toxic effect of copper, but to the selective ion uptake in the course of which sulphuric acid "in statu nascendi" arises beyond the quantity anyhow present owing to the hydrolysis of copper vitriol.

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DIATOMÉES DU PANNONIEN INFÉRIEUR PROVENANT DU BASSIN NÉOGÈNE DE CSÁKVÁR

IIe PARTIE

Par

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(Reçu le 25 mars 1970)

This second part includes a summary of the relics in the order *Pennales* of the phyllum *Bacillariophyta*, as well as a short review of *Phytolitharia, Tintinnidum?* and *Porifera* relics occurring in the assemblage.

On the basis of the per cent evaluation, it is characteristic of the examined deposit association that mesohaline, littoral and plankton form prevail in it.

Actinoptychus trilobatus n. sp. and *Coscinodiscus jambori* n. sp. indicate corroborated by the macrofauna, the Lower Pannonian age and a brackwater facies. *Actinoptychus trilobatus* n. sp. indicates a relationship with the maritime *Actinoptychus senarius* (Ehr.) Ehr.

The site of accumulation of the deposit might have been a pelagic bay slowly separating from the sea, or possibly a lagoon, wherein the water turning fresh was influenced by the nearness of the mainland.

III

Ordre: *Pennales* Schütt 1896
Famille: *Tabellariaceae* Schütt 1896
Genre: *Licmophora* Agardh 1827
Licmophora abbreviata Agardh
Planche VII, Fig. 1—2

1831. *Licmophora abbreviata* Ag. — Consp. crit. diat. p. 42. (non vidi)
1927—1966. *Licmophora abbreviata* Ag. — Hustedt, II. pp. 66—67, Fig. 590.

Longueur de notre échantillon fragmentaire: 55 μ; largeur: 8 μ. En s'adhérant à d'autres Algues, cette forme épiphyte constitue des colonies le long des rivages des mers.

Les fragments seulement de quelques spécimens ont été récoltés à Csákvár, dans les couches du Pannonien inférieur, et notamment: Csákvár, sondage No 9, de 126,6 à 127,7 m, puis Csákvár, sondage No 31, de 262,5 à 265,0 m.

Famille: *Fragilariaceae* (Kützing) De Toni 1892
Genre: *Glyphodesmis* Greville 1862
Glyphodesmis distans (Gregory) Grunow
Planche VII, Fig. 12—14

1857. *Denticula distans* Greg. — Trans. R. Soc. Edinburgh, Bd. 21, Tl. 4. p. 23, T. 2, fig. 36. (non vidi).

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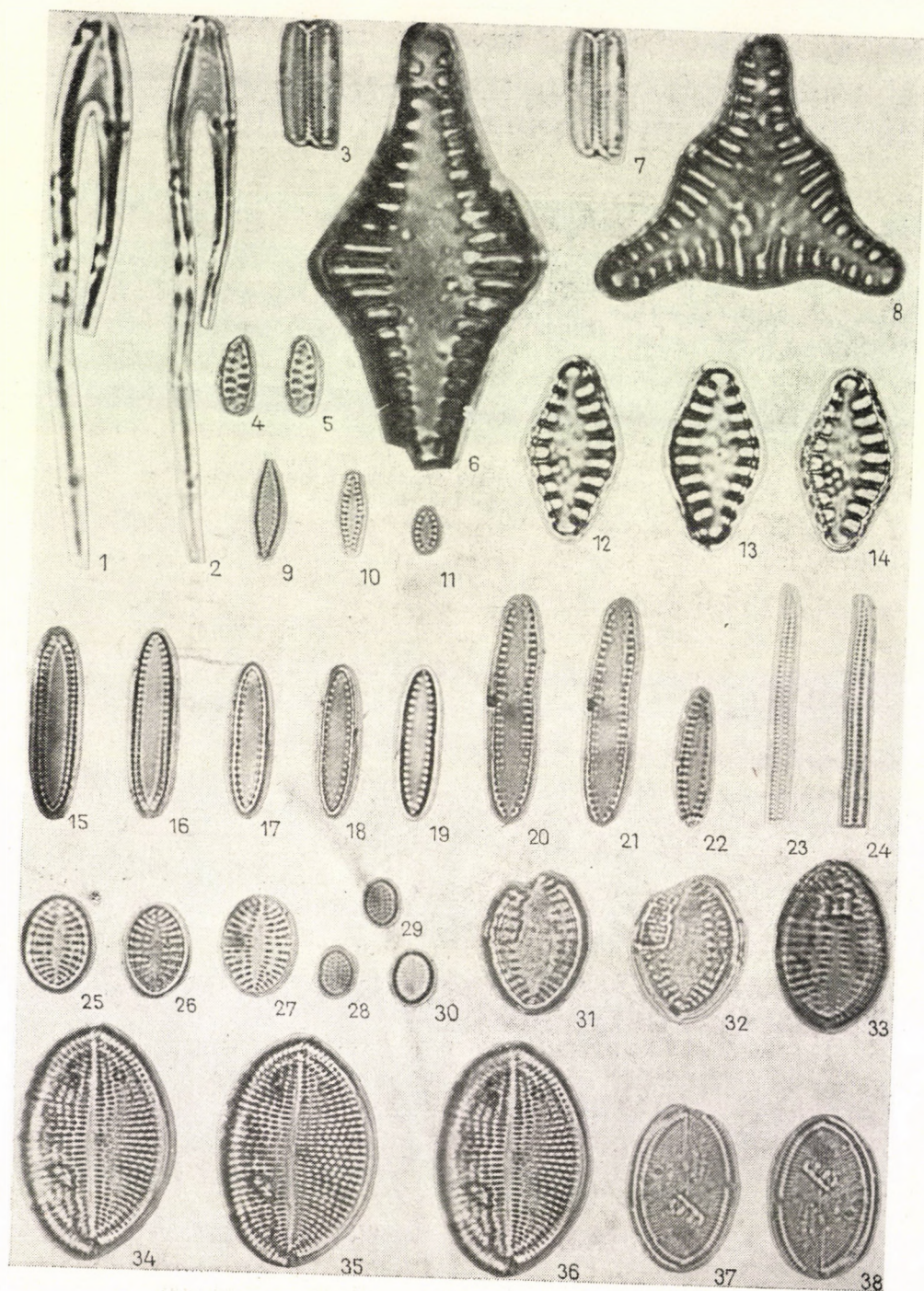
1880—1885. *Glyphodesmis distans* (Greg.) Grun. — in: van Heurck: T. 36, figs. 15—16.

1927—1966. *Glyphodesmis distans* (Greg.) Grun. — Hustedt, II. pp. 125—126, fig. 647.

Longueur: 28 μ, largeur: 14 μ. Les côtes sont robustes, lisses, montrant une légère tendance radiale. 10 μ contiennent 4 côtes.

On la rencontre à Csákvár, sondage No 11, de 184,6 à 186,0 m, dans les couches du Sarmatien supérieur.

C'est une forme littorale qui se retrouve surtout sur les côtes de la Méditerranée dans les baies sableuses aux eaux claires.

Genre: *Opephora* Petit 1888
Opephora martyi Héribaud
Planche VII, Fig. 4—5

1902. *Opephora martyi* Hérib. — Diat. foss. d'Auvergne, I, p. 43, T. 8, fig. 20. (non vidi).

1927—1966. *Opephora martyi* Hérib. — Hustedt II, p. 135, fig. 654.

Longueur: 11 μ, largeur: 5 μ. Pseudoraphé étroit. Nombre des côtes transapicales: 7 tombant sur 10 μ.

Cette espèce se retrouve à Csákvár, sondage No 31, de 256,9 à 261,7 m, dans la couche du Pannonien inférieur. C'est une forme d'eau douce, aussi la rencontre-t-on fréquemment le long des fleuves au courant lent, ou aux rivages lacustres.

Planche VII ×1000

1—2	*Licmophora abbreviata* Ag.	Csv. 31. 262,5—265,0 m
3,7	*Fragilaria brevistriata* Grun.	Csv. 31. 262,5—265,0 m
4—5	*Opephora martyi* Hérib.	Csv. 31. 256,9—261,7 m
6	*Fragilaria leptostauron* (Ehr.) Hust.	Csv. 18. 85,0—96,0 m
8	*Fragilaria leptostauron* (Ehr.) Hust. var. *triangula* n. var.	Csv. 18. 85,0—96,0 m
9—10	*Fragilaria brevistriata* Grun.	Csv. 11. 132,2 m
11	*Fragilaria brevistriata* Grun. var. *elliptica* Hérib.	Csv. 11. 131,9 m
12—14	*Glyphodesmis distans* (Greg.) Grun.	Csv. 11. 184,6—186,0 m
15—16	*Fragilaria lapponica* Grun.	Csv. 11. 184,6—186,0 m
17—19	*Fragilaria lapponica* Grun.	Csv. 31. 262,5—265,0 m
20—21	*Fragilaria estherae* n. sp.	Holotype: Csv. 31. 262,5—265,0 m
22	*Fragilaria estherae* n. sp.	Csv. 11. 132,2 m
23—24	*Synedra* sp.	Csv. 9. 126,6—127,7 m
25—27	*Cocconeis disculoides* Hust.	Csv. 11. 132,2 m
28—30	*Cocconeis scutellum* Ehr. var. *minutissima* Grun.	Csv. 9. 126,6—127,7 m
31—32	*Cocconeis* sp.	Csv. 31. 256,0—256,9 m
33	*Cocconeis disculoides* Hust.	Csv. 9. 126,6—127,7 m
34—36	*Cocconeis placentula* Ehr. var. *intermedia* (Hérib.—Perag.) Cl.	Csv. 9. 144,5 m
37—38	*Cocconeis placentula* Ehr. var. *klinoraphis* Geitl.	Csv. 31. 256,0—256,9 m

Genre: *Fragilaria* Lyngbye 1819
Fragilaria leptostauron (Ehrenberg) Hustedt
Planche VII, Fig. 6

1854. *Biblarium leptostauron* Ehr. T. 12, figs. 35—36.
1909. *Fragilaria tertiaria* Pantocsek — p. 53, Planche II, fig. 20
1927—1966. *Fragilaria leptostauron* (Ehr.) Hustedt II, pp. 153—155, figs. 668. a—f.

La dimension de nos spécimens est beaucoup plus grande que celle de l'espèce typique, et l'ornementation est bien plus grossière. D'après le cachet caractéristique, nos spécimens sont très bien à identifier avec l'espèce typique, ils n'en diffèrent que par leur dimension. Longueur: 51—61 μ, largeur: 30—33 μ. Nombre des côtes transapicales: 3—3,5 à l'intérieur de 10 μ; elles sont bien visibles, à petites lignes très fines d'une légère tendance radiale. Les enveloppes constituent une chaîne continue, s'élargissant en sens transapical. Le pseudoraphé est large, lancéolé. Selon HUSTEDT, 1927—1966 II. p. 154, la longueur des cellules soit 15—30 μ, la largeur: 10—16 μ; le nombre des côtes à l'intérieur de 10 μ: 6—9.

Fragilaria tertiaria de Bucsa (Roumanie) décrite par PANTOCSEK, J. (1909, p. 53, Planche II, fig. 20) dans des sédiments saumâtres du Tertiaire est identifiable à nos spécimens — sauf ses dimensions. Longueur de l'espèce de Bucsa: 32—58 μ, largeur: 16—18 μ, il se trouvent 4 côtes à l'intérieur de 10 μ, lesquelles sont finement striées: «Striae validae, 4 in 10 μ punctatae transversae». (l. c.)

Localité: Csákvár, sondage No 18, de 85,0 à 96,0 m dans la couche du Pannonien inférieur.

Cette espèce constitue des files de chaînes cohérants dans les fonds vaseux des eaux douces limniques.

Fragilaria leptostauron (Ehrenberg) Hustedt
var. **triangula** n. var.
Planche VII, Fig. 8

Type de la variété: préparation de Diatomées No 2160 de l'Institut Géologique de Hongrie. Planche VII., Fig. 8.

Locus typicus: Csákvár, sondage No 18.

Stratum typicum: Csákvár, sondage No 18, de 85,0 à 96,0 m, dans la couche d'aléurite calcaire à Diatomées du Pannonien inférieur.

Description: Notre sujet diffère de l'espèce par sa taille plus grande, les deux côtés sont de 43 μ, le troisième de 41 μ. 10 μ contient 4—4,5 côtes finement striées. On trouve 25 à 30 petites lignes délicates à l'intérieur de 10 μ. Les côtes sont inégales: elles sont minces et pointues, ou grosses et obtuses, puis s'amincissantes et se penchant en arc vers les pôles. Les pôles se trouvent légèrement arrondis, les faces latérales présentent des arcs convexes. Le pseudoraphé

est triangulaire et s'étend jusqu'aux pôles en y composant une connexion. Le champ hyalin du pseudoraphé n'est pas tout à fait lisse, il se montre très légèrement froncé, comme portant quasiment une continuation des côtes. L'épaisseur de la paroi: 1 μ.

Remarque: Notre échantillon diffère du type par sa forme triangulaire, à trois pôles. Correspondant à cette forme, les côtes se placent en arcs autour des trois pôles. Ces côtes sont bien plus inégales que celles de l'espèce: plus pointues, plus obtuses et moins denses. Le pseudoraphé montre dans le sens des côtes, comme leurs continuations, des fins plissements, des froissements légers, tandis que ce champ est lisse chez le type.

Localité: Csákvár, sondage No 18, de 85,0 à 96,0 m, dans la couche du Pannonien inférieur. Cette forme se retrouve ensemble avec les spécimens à grande taille de l'espèce. Un seul spécimen.

Fragilaria construens (Ehrenberg) Grunow

1841. *Staurosira construens* Ehr. — Abh. Berl. Akad. p. 424. (non vidi).
1862. *Fragilaria construens* (Ehr.) Grun. — p. 371. fig. 10.
1927—1966. *Fragilaria construens* (Ehr.) Grun. — Hustedt II, pp. 156—158, figs. 670, a—c.

Cette forme se retrouve très rarement à Csákvár, dans le sondage No 18, de 85,0 à 96,0 m et Csákvár, sondage No 31, de 262,5 à 265,0 m dans la couche du Pannonien inférieur.

Fragilaria brevistriata Grunow
Planche VII, Fig. 3, 7, 9—10

1880—1885. *Fragilaria brevistriata* Grun. — In: Van Heurck, Taf. 45, Figs 32, 34.
1927—1966. *Fragilaria brevistriata* Grun. — Hustedt II, pp. 168—169, Figs. 676 a—e.
1968/a. *Fragilaria brevistriata* Grun. — Hajós p. 153.

Longueur des cellules: 13—17 μ, hauteur: 3—4 μ, largeur: 3,5—4 μ. Les côtes sont courtes. Le bord de la paroi est ornée par des petits points, des côtes dont on trouve 13 à l'intérieur de 10 μ.

Localité Csákvár, sondage No 9, de 126,6 à 127,7 m. Csákvár, sondage No 11, 132,2 m. Csákvár, sondage No 31, de 256,0 à 256,9 et de 262,5 à 265,0 m dans la couche du Pannonien inférieur. C'est une forme d'eau douce qui témoigne un rivage très proche.

Fragilaria brevistriata Grunow var. *elliptica* Héribaud
Planche VII, Fig. 11

1903. *Fragilaria brevistriata* Grun. var. *elliptica* Hérib. — Diat. foss. d'Auvergne, Bd. II, p. 74, Taf. 10, Fig. 11. (non vidi).

1927—1966. *Fragilaria brevistriata* Grun. var. *elliptica* Hérib. — Hustedt II. p. 169, fig. 676 f.

Les variétés à 7—8 μ se retrouvent ensemble avec l'espèce à Csákvár, sondage No 11, 131,9 m, dans la couche du Pannonien inférieur.

Fragilaria lapponica Grunow
Planche VII, Fig. 15—19

1880—1885. *Fragilaria lapponica* Grun. — In: Van Heurck, Taf. 45, fig. 35.
1927—1966. *Fragilaria lapponica* Grun. — Hustedt II, pp. 170—172. fig. 678.

Longueur des cellules: 21—27 μ, largeur: 5—10 μ. Les côtes sont courtes, et se placent le long de la bordure de la frustule; on en trouve 9—9,5 par 10 μ, en forme des points.

Localité: Csákvár, sondage No 9, de 126,6 à 127,7 m; Csákvár, sondage No 31, de 256,0 à 256,9 m, de 256,9 à 261,7 m, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur, et de Csákvár No 11, de 184,6 à 186,0 m dans le Sarmatien supérieur.

Forme fréquente dans des eaux lacustres ou des rivières au cours lent.

Fragilaria estherae n. sp.
Planche VII, Fig. 20—22

Derivatio nominis: de Mme ESZTER NAGY Professeur palynologiste, chef du Département de Paléontologie de l'Institut Géologique de Hongrie, (Budapest).

Holotypus: Institut Géologique de Hongrie — Département de Paléontologie: préparation de Diatomées No 2032/2; Planche VII., Fig. 20—21.

Locus typicus: Csákvár, sondage No 31.

Stratum typicum: Csákvár, sondage No 31, de 262,5 à 265,0 m, dans la couche diatomique du Pannonien inférieur.

Description-diagnostique: La cellule se trouve longue, parallèle, aux côtés un peu déprimés ou légèrement rétrécie, se terminant en lanciforme arrondie.

Holotypus: Longueur: 32 μ, largeur: 6 μ. Côtes à fines ponctuations se rangeant perpendiculairement aux bords de la cellule et parallèles entre elles mais à longueur inégale. On trouve 10 côtes à l'intérieur de 10 μ, et 1 à 3 point dans une côte. Pseudoraphé large, lancéolé.

Differentalis-diagnosis: Elle se trouve la plus proche à de *Fragilaria lapponica* Grun — in Van Heurck, 1880—1885. T. 45. Fig. 35. d'après sa dimension et sa forme, et le nombre de ses côtes. Elle en diffère considérablement par la forme des côtes qui se montrent sur nos spécimens non petites comme des points, mais minces, de longueur inégale, ornées de points bien visibles.

Dimension: Longueur: 18,4—32 μ, largeur: 5—6 μ. Nombre des côtes transapicales: 10 sur 10 μ.

Localité: Csákvár, sondage No 11, 132,2 m, Csákvár, sondage No 18, de 85,0 à 96,0, Csákvár, sondage No 31, de 256,9 à 261,7 m et de 262,5 à 265,0 m dans la couche du Pannonien inférieur.

Genre: *Synedra* Ehrenberg 1830
Synedra sp.
Planche VII, Fig. 23—24

Fragment. Longueur: 36 μ, largeur: 2,5—3 μ. La bordure de la cellule porte des petites lignes courtes, délicates, il en tombe 14 sur 10 μ.

Csákvár, sondage No 9, de 126,6 à 127,7 m, dans la couche du Pannonien inférieur, il en ne provient que quelques fragments.

Famille: *Achnanthaceae* (Kützing) Grunow 1880
Genre: *Cocconeis* Ehrenberg 1838
Cocconeis scutellum Ehrenberg var. *minutissima* Grunow
Planche VII, Fig. 28—30

1880—1885. *Cocconeis scutellum* Ehr. var. *minutissima* Grun. — in: Van Heurck Taf. 29, Fig. 12.

1927—1966. *Cocconeis scutellum* Ehr. var. *minutissima* Grun. — Hustedt II. p. 339.

Petites cellules. Longueur: 6,4—7 μ, largeur: 5—5,5 μ.

A Csákvár on en retrouve sporadiquement quelques spécimens et notamment: Csákvár, sondage no 9, de 126,6 à 127,7 m, Csákvár, sondage No 18, de 85,0 à 96,0 m, et Csákvár, sondage No 31, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur.

Forme littorale, épiphyte, laquelle, quoique bien plus petite, soit bien difficile à distinguer de la forme *Cocceneis scutellum* Ehr. var. *parva* Grunow — in: VAN HEURCK, 1880—85. Taf. 29., Fig. 8—9. Leur répartition, selon HUSTEDT, F. 1927—1966. II. p. 339: «var. parva auch an salzhaltigen Stellen des Binnenlandes. Var. *minutissima* von GRUNOW bei FRANZ-JOSEFS Land gefunden, aber wohl weiter verbreitet.»

Cocconeis disculoides Hustedt
Planche VII, Fig. 25—27, 33

1955. *Cocconeis disculoides* Hustedt — p. 17, Pl. 5, figs. 8—11, Pl. 7, fig. 8.

Nos spécimens sont relativement plus petits que ceux que HUSTEDT eut décrit. On n'a retrouvé que des frustules pleurovalvaires de longueur 14—

24 μ et de largeur: 9—16 μ. Nous les avons differenciés du *Cocconeis disculus* (Schum.) Cleve 1894 — 95, p. 172 — espèce d'eau douce — sur la base de la description de HUSTEDT l. c.: «transapical striae coarse, slightly radiate, 8—10 in 10 μ delicately punctate.» HUSTEDT avait déterminé cette espèce dans un échantillon de vase provenant de la Caroline du Nord (Golfe de BEAUFORT).

Localité: Csákvár, sondage No 9, de 126,6 à 127,7 m, Csákvár, sondage No 11, 131,9 m et 132,2 m, dans la couche du Pannonien inférieur.

Cocconeis placentula Ehrenberg var. *klinoraphis* Geitler
Planche VII, Fig. 37—38

1927. *Cocconeis placentula* Ehr. var. *klinoraphis* Geitl. — Arch. f. Protistenkunde, Bd. 59. p. 514, Textfig. 2a, b, T. 12, Fig. 1. (non vidi).
1927—1966. *Cocconeis placentula* Ehr. var. *klinoraphis* Geitl. — Hustedt II, p. 348, fig. 803.

Longueur raphovalvaire 24 μ, largeur 16 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Forme épiphyte d'eau douce.

Cocconeis placentula Ehrenberg var. *lineata* (Ehrenberg) Cleve
Planche VIII, Fig. 1—2

1843. *Cocconeis lineata* Ehr. — Abh. Berl. Akad. (1841) p. 81. (non vidi).
1894—1895. *Cocconeis placentula* Ehr. var. *lineata* (Ehr.) Cl. II. p. 169.
1927—1966. *Cocconeis placentula* Ehr. var. *lineata* (Ehr.) Cl. — Hustedt II, pp. 348—349, fig. 802. d.

La pleurovalve figurée est de longueur 68 μ, et de largeur 41 μ. 10 μ contiennent 19—20 lignes ponctuées se disposant en arcs radiaires, entre-croisés par des côtes hyalines longitudinales, ondoyantes.

Localité: Csákvár, sondage No 18, de 85,0 à 96,0 m, et Csákvár, sondage No 31, de 256,0 à 256,9 m dans la couche du Pannonien inférieur.

Forme épiphyte, fréquente dans les eaux douces.

Cocconeis placentula Ehrenberg var. *intermedia* (Héribaud et Peragallo) Cleve
Planche VII, Fig. 34—36

1893. *Cocconeis intermedia* Hérib. et Perag. — Diat. d'Auvergne p. 44, T. 3, fig. 1—2. (non vidi).
1894—1895. *Cocconeis placentula* Ehr. var. *intermedia* (Hérib. et Perag.) Cleve II. p. 169.
1927—1966. *Cocconeis placentula* Ehr. var. *intermedia* (Hérib. et Perag.) Cl. — Hustedt II. p. 348.

Longueur de la cellule: 34 μ, largeur: 22 μ. Notre spécimen représente une forme intermédiaire entre cette espèce très variable, et notamment entre celle de var. *euglypta* et var. *lineata*, formes décrites par HUSTEDT, 1927—1966 II. p. 347, selon lequel: «die lediglich auf der Streifenzahl begründeten Varietäten (var. *intermedia* und var. *Rouxii*) sind m. E. am besten aufzugeben».

Cette forme se rencontre à Csákvár, sondage No 9, 144,5 m, dans la couche du Pannonien inférieur.

Forme épiphyte d'eaux douce.

Cocconeis sp.
Planche VII, Fig. 31—32

Ce fragment de pleurovalve de mauvaise conservation montre une longueur de 20 μ. Le pseudoraphé est largement lancéolé. Les côtes présentent des arcs radiaires, leur nombre — au milieu de la cellule — est 7,5, à l'intérieur de 10 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m dans la couche du Pannonien inférieur.

Genre: *Achnanthes* Bory 1822
Achnanthes delicatula (Kützing) Grunow
Planche VIII, Fig. 9—10

1844. *Achnanthidium delicatulum* Kütz. — Bac. p. 75, Taf. 3, Fig. 21. (non vidi).
1880. *Achnanthes delicatula* (Kütz.) Grun. — in: Cleve et Grun., p. 22.
1927—1966. *Achnanthes delicatula* (Kütz.) Grun. — Hustedt II, pp. 389—390, Fig. 836.

Longueur des frustules: 10—12 μ, largeur: 5—6 μ. Les spécimens répondent à l'espèce typique.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Espèce mésohalobe, euryhaline. L'espèce se retrouve dans des eaux salées, littorales, isolées, on les rencontre aussi dans des eaux douces.

Achnanthes lanceolata (Brébisson) Grunow
Planche VIII, Fig. 7—8

1849. *Achnanthidium lanceolatum* Bréb. — Kützing p. 54.
1880. *Achnanthes lanceolata* (Bréb.) Grun. — in: Cleve et Grun. p. 23.
1927—1966. *Achnanthes lanceolata* (Bréb.) Grun. — Hustedt II, pp. 408—411, Figs. 863. a—d.

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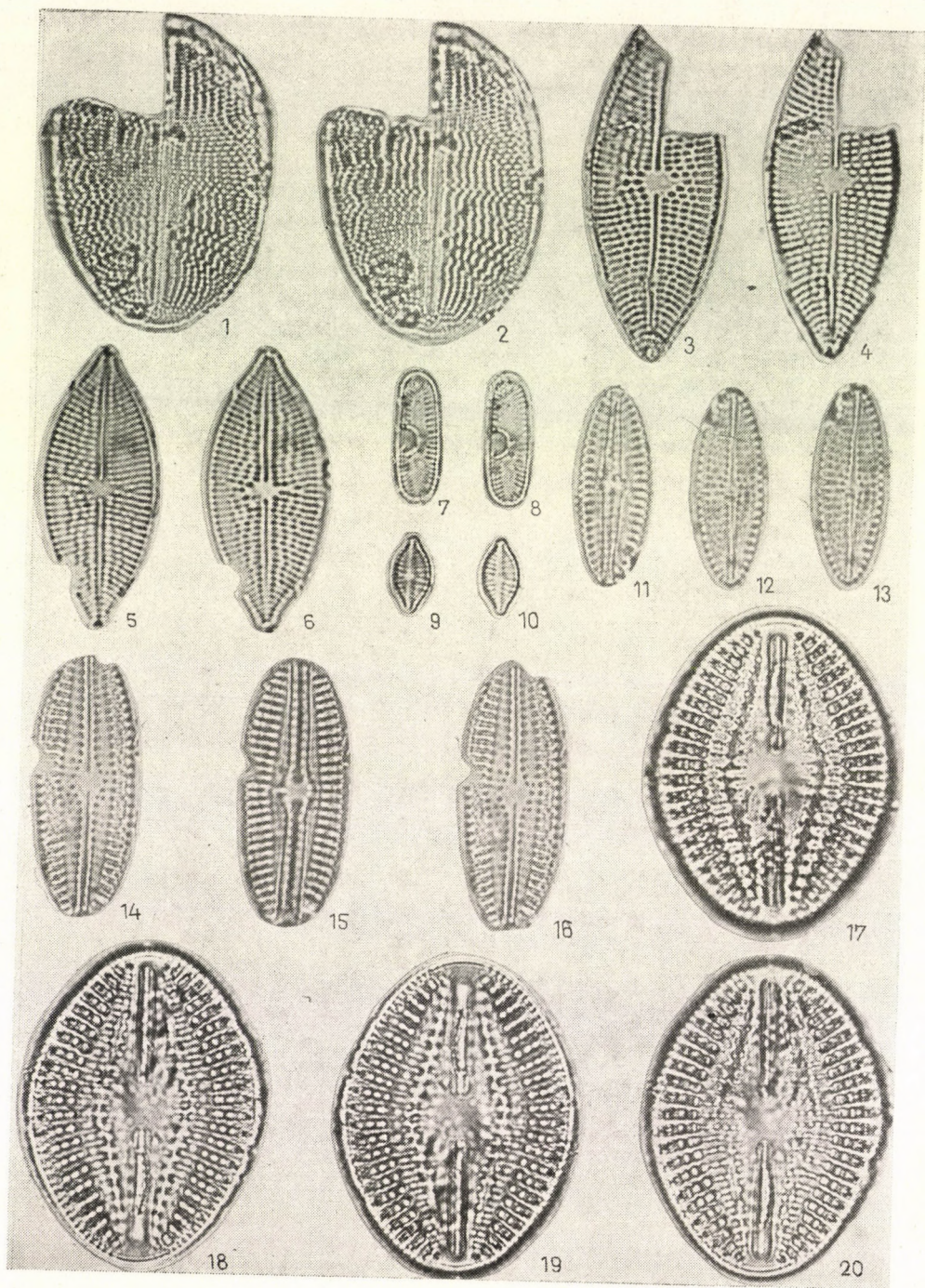
Longueur: 19—20 μ, largeur: 7 μ. 10 μ contient 14 côtes courtes, transapicales en arcs radiaires.

Localité: Csákvár, sondage No 11, 132,2 m, dans la couche du Pannonien inférieur.

Espèce répandue dans les eaux douces.

Famille: *Naviculaceae* Schütt 1896
Genre: *Mastogloia* Thwaites 1896
Mastogloia tuscula (Ehrenberg) n. comb.
Planche VIII, Fig. 3—6

1880—1885. *Navicula tuscula* (Ehr.) Van Heurck, p. 95, Pl. 10., Fig. 14.

La frustule se trouve lancéolé, un peu allongée, à bouts en bec. Longueur: 40—52 μ, largeur: 17—20 μ. Raphé un peu tordu. Le champ axial est étroit, rondelet, asymétrique, s'élargissant en formant un champ central. Les côtes transapicales, vers les bouts de la cellule, montrent une tendance d'arc radiaire, tandis qu'au milieu de la cellule elles se montrent convergentes, courtes ou longues, en alternant. 10 μ contient 10 côtes transapicales. Les côtes sont croisées par des côtes longitudinales, ondoyantes, — parallèles à l'axe longitudinale et suivant l'élargissement autour de l'aréa centrale dévient vers le rebord de la cellule. Là, le long du bord, elles produisent — en s'alternant — une double ponctuation. L'anneau à logettes marginales est étroit, les logettes sont de grandeur égale.

Localité: Csákvár, sondage No 11, de 184,6 à 186,0 m, dans la couche du Sarmatien supérieur et Csákvár, sondage No 18, de 85,0 à 96,0 m dans la couche du Pannonien inférieur.

Remarque: La révision et la liste de synonymie complète sera publiée dans une étude à part, fondée sur l'analyse des espèces originales décrites par Pantocsek et Grunow.

Planche VIII ×1000

1—2	*Cocconeis placentula* Ehr. var. *lineata* (Ehr.) Cl.	Csv. 31. 256,0—256,9 m
3—6	*Mastogloia tuscula* (Ehr.) n. comb.	Csv. 11. 184,6—186,0 m
7—8	*Achnanthes lanceolata* (Bréb.) Grun.	Csv. 11. 132,2 m
9—10	*Achnanthes delicatula* (Kütz.) Grun.	Csv. 31. 256,0—256,9 m
11—16	*Diploneis mauleri* (Brun) Cl.	Csv. 31. 256,0—256,9 m
17—20	*Diploneis soói* n. sp.	Holotype; Csv. 31. 256,0—256,9 m

Genre: *Diploneis* Ehrenberg 1844
Diploneis mauleri (Brun) Cleve
Planche VIII, Fig. 11—16

1880. *Navicula mauleri* Brun. — Diat. d. Alp. p. 77, T. 1, Fig. 18. (non vidi).
1894—1895. *Diploneis mauleri* (Brun) Cleve I. p. 98.
1927—1966. *Diploneis mauleri* (Brun) Cl. — Hustedt II, p. 639, fig. 1046.

Le nombre des côtes transapicales se trouve rangée en 7—8 à l'intérieur de 10 μ. On voit, entre les côtes, s'aligner des aréoles en double rangs. Selon HUSTEDT (l. c.): «Längskanäle in der Aussenwand mit grösseren Tüpfeln, die gewöhnlich in zwei längsreihen geordnet sind.»

Localité: Csákvár, sondage No 31, de 256,0 à 256,9, dans la couche du Pannonien inférieur.

La forme récente de l'espèce est fréquente dans le fond vaseux des eaux douces lacustres. C'est la forme caractéristique de la flore à Ancylus.

Diploneis soói n. sp.
Planche VIII, Fig. 17—20
Planche IX, Fig. 1—3

Derivatio nominis: En honneur de Monsieur le Prof. Rezső Soó, membre de l'Académie des Sciences Hongroise.

Holotypus: Institut Géologique de Hongrie — Département de Paléontologie: Préparation diatomique No 2029; photo-microscope Opton: Planche VIII, Fig. 17—20.

Locus typicus: Csákvár, sondage No 31.

Stratum typicum: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche d'aléurite à Diatomées du Pannonien inférieur.

Description-diagnostique: La frustule est très large, elliptique, s'arrondissant au bouts. Longueur de l'Holotype 46 μ, largeur: 35 μ. La varice centrale se trouve grande, rondelette ou allongée en sens apical; elle est lancéolée, courte. Les canaux longitudinaux s'élargissent en arcs vers le milieu, se rétrécissant vers les bouts, délimitent ainsi un champ lancéolé. Le raphé est droit, étant entouré d'une corne longitudinale s'élargissant aux bouts et au milieu. La surface valvaire est ornée de côtes radiales un peu arquées. 10 μ contiennent 4—4,5 côtes, dont la partie extérieure se recouvre de nombreuses côtes longitudinales, à peu près à la distance des côtes transapicales. Par ce fait les champs presque carrés sont séparés par un épaississement de la paroi entre les côtes longitudinales. La paroi extérieure des champs carrés est percée par quatre pores (Fig. 6/a.). Et là, on trouve une ouverture d'aréole rondelette c'est-à-dire sur chaque côte s'alignent des rangées d'aréoles rondelettes et bien développées (Fig. 6/b.). Un rangée compte 6—7 aréoles par 10 μ. Ces aréoles se montrent vers le milieu de la frustule — à l'intérieur du canal longitudinal — plus petites, parfois doubles, et les rangées se terminent irrégulièrement pliées. Sur le bord périphérique de la frustule, le long de la ligne qui la double parallèlement, les aréoles se présentent également plus petites, et en fourchant, continuent en doubles rangs. Auprès des bouts arrondis de la cellule, les courtes rangées aréolaires renferment de chaque côte un champ lisse en éventail.

Differentialis-diagnosis: Cette forme se trouve la plus avoisinée de celle décrite de PANTOCSEK 1886: p. 28, T. 13, Fig. 109, *Navicula pseudofusca* — espèce fossile — laquelle a été présentée par HUSTEDT 1927—1966: II. p. 656, Fig. 1056, comme *Diploneis fusca* (Pant.) Cl. var. *pseudofusca* (Pant.) Cleve. Cette forme ne peut être identifiée avec la nôtre, mais l'affinité est indubitablement certaine. Différence essentielle: tandis que la paroi extérieure de *Diploneis fusca* var. *pseudofusca* présente des pores fins, serrés, notre *Diploneis soói* montre entre ses côtes dans les carrés à parois épaissie des pores plus grossiers dans la paroi extérieure et des ouvertures aréolaires régulières dans celle intérieure. Puis, les cellules qui se trouvent dans les sédiments d'ici sont plus petits, les cornes moins robustes, plus courtes, l'ornement plus grossier, le nombre des aréoles et des côtes se font plus rares, le raphé est plus court, et les bouts à champs lisses sont plus étendues que chez l'espèce décrite par HUSTEDT ou chez celle par PANTOCSEK. Selon HUSTEDT on rencontre l'espèce littorale dans la Méditerranée.

Dimension: Longueur: 46—64 μ, largeur: 35—42 μ.

Localité: Csákvár, sondage No 9, de 126,6 à 127,7 m, Csákvár, sondage No 11, de 132,2 m; Csákvár, sondage No 31, de 256,0 à 256,9 m et Csákvár, sondage no 18, de 85,0 à 96,0 m dans la couche du Pannonien inférieur.

Remarque: Notre espèce est une telle forme saumâtre, se révèle la modification de la forme et de l'ornementation, changements qui se montrent en proportion de la perte de salinité. La cellule devient plus courte en sens de l'axe longitudinal, tandis qu'elle s'élargit en sens transapical. Les formes récente et fossile de Diploneis fusca var. pseudofusca sont celles littorales. Il est indubitable que notre espèce ait un rapport génétique. La variation a dû s'accomplir par la perte de salinité de la mer.

Diploneis ovalis (Hilse) Cleve
Planche IX, Fig. 4—8

1861. *Pinnularia ovalis* Hilse — in RABENHORST, Alg. Eur. Nr. 1025. (non vidi).

1891. *Diploneis ovalis* (Hilse) Cleve — Diat. Finl. p. 44, T. 2, Fig. 13. (non vidi).

1927—1966. *Diploneis ovalis* (Hilse) Cleve — Hustedt II, pp. 671—673, Fig. 1065 a—e.

Longueur des frustules: 32—48 μ, largeur: 18—22 μ. Nombre des côtes transapicales: 8—10 à l'intérieur de 10 μ. Les points ornant les côtes deviennent toujours plus petits vers le bord de la frustule; 10 μ contiennent 10—12 points.

Localité: Csákvár, sondage No 11, de 184,6 à 186,0 m, dans le Sarmatien supérieur, et Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Les spécimens fossiles diffèrent en tant des récents que le nombre des côtes transapicales se fait plus rare. Selon l'analogie récente, c'est une forme d'eau peu salée, aérophile. Nous en avons peu rencontrée.

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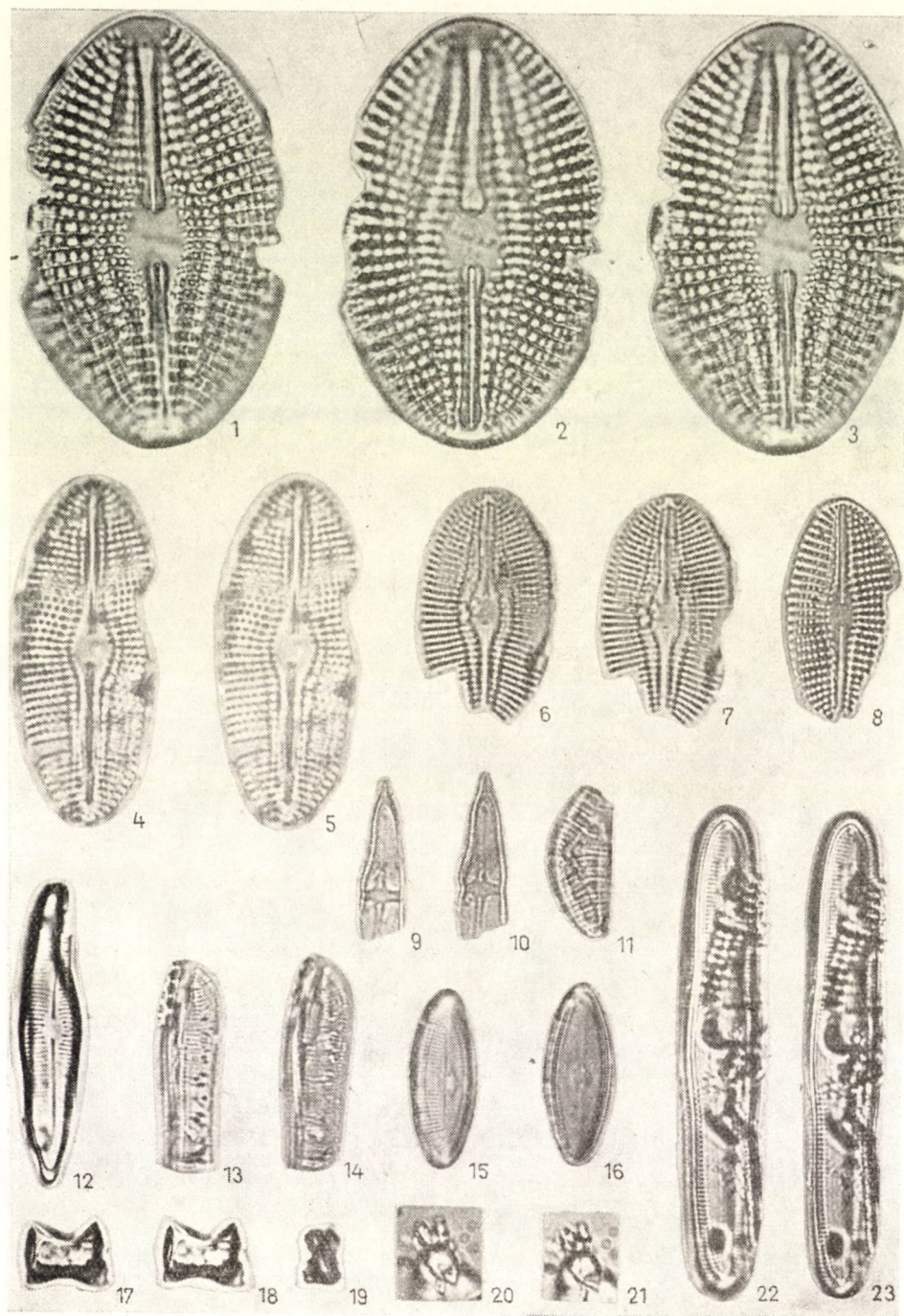
Genre: *Stauroneis* Ehrenberg 1843
Stauroneis smithii Grunow
Planche IX, Fig. 9—10

1860. *Stauroneis smithii* Grun. — p. 564, T. 6, Fig. 6.
1927—1966. *Stauroneis smithii* Grun. — Hustedt II, pp. 810—913, Fig. 1157.

On n'en a trouvé qu'une frustule fragmentaire dont la longueur est de 23 μ, et la largeur de 6—7 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

C'est une espèce d'eau douce, partout répandue, dont ce seul spécimen a dû en être lavé.

Genre: *Navicula* Bory 1824
Navicula sp.
Planche IX, Fig. 12

Un seul spécimen de mauvaise conservation a été trouvé à Csákvár: sondage No 31, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur.

Genre: *Caloneis* Cleve 1894
Caloneis sp. I.
Planche IX, Fig. 15—16

Forme elliptique. Longueur: 27 μ; largeur: 10 μ. La valve porte 18 minces côtes arquées. Le raphé est aussi mince, droit. Au milieu de la frustule on aperçoit une aréa centrale rondelette où un arc hyaline rallie les deux bouts centraux déclinants du raphé.

Localité: Csákvár, sondage No 11, à 131,9 m, dans la couche du Pannonien inférieur.

Forme du fond des eaux salées et aussi des eaux douces.

Planche IX ×1000

1—3	*Diploneis soói* n. sp.	Csv. 11. 132,2 m
4—5,8	*Diploneis ovalis* (Hilse) Cl.	Csv. 31. 256,0—256,9 m
6—7	*Diploneis ovalis* (Hilse) Cl.	Csv. 11. 184,6—186,0 m
9—10	*Stauroneis smithii* Grun.	Csv. 31. 256,0—256,9 m
11	*Epithemia salina* Pant.	Csv. 11. 131,9 m
12	*Navicula* sp.	Csv. 31. 262,5—265,0 m
13—14	*Nitzschia* sp. II.	Csv. 31. 262,5—265,0 m
15—16	*Caloneis* sp. I.	Csv. 11. 131,9 m
17—18	*Lithodontium* (Phytolitharia)	Csv. 31. 256,9—261,7 m
19	*Lithodontium* (Phytolitharia)	Csv. 31. 262,5—265,0 m
20—21	*Tintinnidium?* sp. (Ciliata)	Csv. 31. 262,5—265,0 m
22—23	*Caloneis* sp. II.	Csv. 31. 256,0—256,9 m

Caloneis sp. II.
Planche IX, Fig. 22—23

Frustules longues, droites, à peine s'élargissant au milieu de la cellule. Longueur: 69 μ, largeur: 9 μ, largeur du centre: 11 μ. A l'intérieur de 10 μ 17 côtes très minces, à ponctuation très fine, un peu écartées aux bouts, les décorent. L'aréa centrale est grande, s'étend jusqu'au bord de la frustule.

Localité: dans la couche du Pannonien inférieur, sondage de Csákvár No 31, de 256,0 à 256,9 m. Forme benthique d'eau salée aussi bien que d'eau douce, et indique un dépôt d'eau peu profonde.

Genre: *Epithemia* Brébisson 1838
Epithemia salina Pantocsek
Planche IX, Fig. 11

1889. *Epithemia salina* Pantocsek II. p. 61., Tab. 7, Fig. 131.
1968/a. *Epithemia salina* Pant. — Hajós p. 197, Taf. LVII, Fig. 27—31.

Les spécimens fragmentaires de cette espèce proviennent de la couche du Pannonien inférieur de Csákvár. Sondage No 11, 131,9 m. L'espèce indique un milieu peu salé et peu profond. C'est une épiphyte vivant en s'adhérant contre aux Végétaux.

Pantocsek (l. c) l'a décrit dans les dépôts peu salé du Miocène de Szücsi et de Gyöngyöspata.

Genre: *Nitzschia* Hassal 1845
Nitzschia sp. I.
Planche X, Fig. 1

Ce fragment de cellule est long, un peu ondoyant. Longueur: 100 μ, largeur: 7 μ. La surface se trouve ornée de côtes disposées serrées, à ponctuation très fine. Nombre des points marginaux en tête de ces côtes transversales: 6 à l'intérieur de 10 μ.

La localité de notre spécimen est à Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Nitzschia sp. II.
Planche IX, Fig. 13—14

On a retrouvé seulement un fragment de cette forme. La surface valvaire se recouvre de côtes à ponctuation très fine. Les points marginaux de cet ornement pointillé change en petites lignes de différentes longueur et de densité irrégulière. Longueur: 30 μ, largeur: 8—9 μ.

La localité de l'échantillon se trouve à Csákvár, sondage No 31, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur.

Genre: *Surirella* Turpin 1829
Surirella oblongella n. sp.
Planche X, Fig. 2—3

Holotypus: Institut Géologique de Hongrie — Département de Paléontologie: Préparation de Diatomées No 2030/1; photo-microscope Opton: 9,6—121,0; planche X., Fig. 2—3.

Locus typicus: Csákvár, sondage No 31.

Stratum typicum: Csákvár, sondage No 31, de 256,0 à 256,9 m dans le Pannonien inférieur, dans la couche d'aléurite diatomique.

Description-diagnostique: les frustules montrent une hétéropolarité à peine visible; elles sont longues, elliptiques, aux côtés délicatement arqués, et aux bouts obtus, lancéolés. Longueur: 85 μ, largeur: 24 μ. Le canal des ailes est bien développé, bien plus étroit que les «fenêtres». A l'intérieur de 100 μ se trouvent 20 canaux. La surface de la frustule est à peine onduleuse. Les côtes sont larges, finement ornées de points et de petites lignes; elles sont arrondies vers la ligne médiane. Au bout de chaque champ lisse se trouvant entre les côtes, s'élève une épine. Pour ces épines il n'y a ni dimension, ni forme, ni hauteur, ni même disposition qui en soient régulières. L'une est aussi petite qu'un point, l'autre se trouve allongée et robuste. Elles sont disposées du côté droit et gauche de la ligne médiane apicale de la frustule, toujours à la hauteur des «fenêtres», dans des distances de 1—2 μ.

Differentialis-diagnosis: Notre spécimen se trouve le plus proche de l'espèce *Surirella elegantula* Hustedt (Huber—Pestalozzi, 1942, p. 512, Abb. 623. B) collectionnées dans les lacs Tovoet et Matano de Célébès. Différences essentielles qui les séparent du nôtre: l'espèce de Csákvár a le milieu tout lisse, tandis que celle décrite par Hustedt (l.c.): «Mitellinie stark gezähnt», ensuite les champs d'entre les côtes sont lisses, enfin, les bouts des côtes ne portent point d'épines.

Dimension: longuer: 85 μ, largeur: 24 μ, 100 μ contiennent 20 côtes, 20 canaux d'aile, puis 20 "fenêtres", et tout autent d'épines entre les côtes.

Localitè: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannoni, en inférieur.

Incertae sedis: *Phytolitharia* Ehrenberg 1854
Lithodontium Ehrenberg 1841
Planche IX, Fig. 17—19

Tests opalins tout-petits, anguleux, plats, rétrécies au milieu: phytolithes opales. Leur forme est irrégulière.

Dimension: Longueur: 8—12 μ, largeur: 5—10 μ, auprès de la rétrécissement: 3—5 μ.

Localité: Csákvár, sondage No 31, de 256,9 à 261,7 m, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur.

Remarque: D'après nos précédentes analyses micropaléontologiques, de tels petits tests de phytolithes opales ont été collectionnées — et en assez grande quantité — dans les dépôts diatomiques du Pliocène de la Montagne de Tokaj (prononcer: Tokay). (Hajós 1968/b p. 225, Planche I., Fig. 1—21; Planche II, Fig. 1—10.) Les phytolithes opales témoignent toujours des dépôts littoraux d'eau peu profonde (l. c. p. 228).

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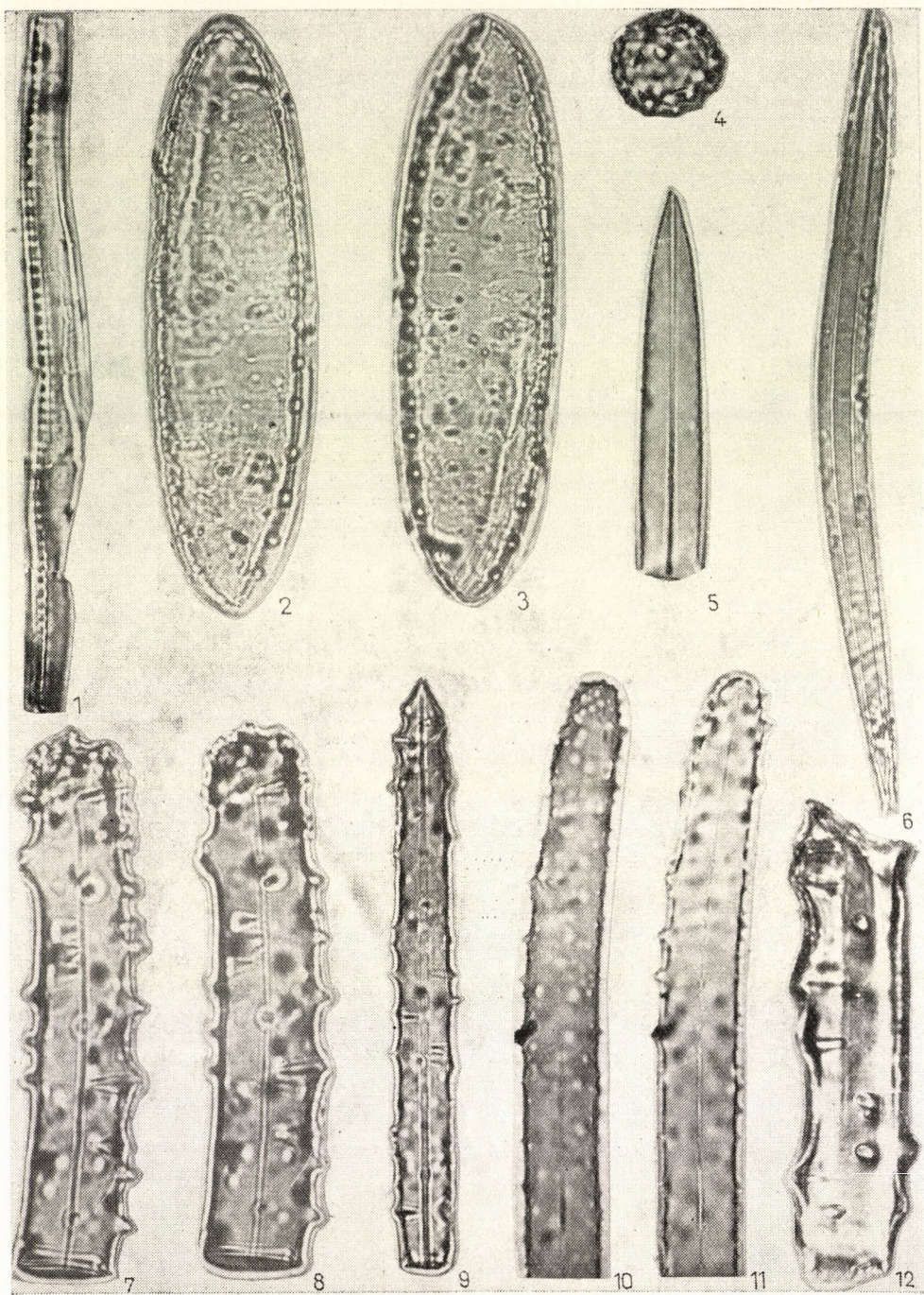
Tribu: *Protozoa* Goldfuss 1818
Classe: *Ciliata* Perty 1852
Tintinnidium? sp.
Planche IX, Fig. 20—21

Le calice siliceux devenant vite aiguisé est de longueur de 6 μ, la largeur en est 4 μ. De l'ouverture à rebord rectiligne, s'allongent de nombreux cils vibratiles, de longueur de 4 à 5 μ.

Localité: Csákvár, sondage No 31, de 262,5 à 265,0 m, dans la couche du Pannonien inférieur.

Remarque: Nous avons déjà rencontré et analysé des ciliés semblables dans le Tortonien supérieur à Diatomées dans l'avant-pays de la Montagne de Mátra, dans les confins de Szurdokpüspöki, dans la tranchée du chemin de fer industriel, et également à Szurdokpüspöki, dans le sondage No 6., en profondeur de 6 m. Pour l'ordre de grandeur et la construction, ces spécimens sont fort semblables, bien que leur forme et leur «calice» soient très variables; mais tous — sans exception — proviennent de littoraux peu ou à peine salés en compagnie d'associations de Diatomées et de Phytolithaires. D'après leurs formes, on doit conclure qu'ils étaient sessiles. Ils s'avèrent comme excellents marqueurs de faciès.

D'après les cachets observés, les débris fossiles analysés jusqu'à présent, se montrent le plus proche au genre *Tintinnidium* Stein 1863 d'eau douce, mais en diffèrent en ordre de grandeur — nos spécimens étant beaucoup plus petits. Selon Kahl, A. 1930 p. 516 les spécimens qu'il décrit montrent une taille de longueur de 35 à 50 μ, tandis que les nôtres sont de dimension si menue qu'aucune ne surpasse la longueur de 15 μ. La plupart présente 10—12 μ.

Ordre: *Porifera* Grant 1872
Classe: *Desmospongea* Sellas 1875
Megasclera débris
Sphaeraster
Planche X, Fig. 4

Débris sphérique, couvert d'épines obtuses. Diamètre: 16 μ, hauteur des épines proéminentes 1—2 μ; selon Hajós M. 1968/a p. 212.: «mit zahlrei-

Planche X ×1000

1	*Nitzschia* sp. I.	Csv. 31. 256,0—256,9 m
2—3	*Surirella oblongella* n. sp.	Holotype; Csv. 31. 256,0—256,9 m
4	*Sphaeraster*	Csv. 11. 131,9 m
5	*Monaxon, oxea* I. fragment	Csv. 11. 132,2 m
6	*Monaxon, oxea* II.	Csv. 31. 256,0—256,9 m
7—8	*Monaxon, acanthostyl* I. fragment	Csv. 31. 256,0—256,9 m
9	*Monaxon, acanthostyl* IV. fragment	Csv. 130,0 m
10—11	*Monaxon, acanthostyl* III. fragment	Csv. 11. 132,2 m
12	*Monaxon, acanthostyl* II. fragment	Csv. 31. 256,0—256,9 m

chen Stacheln bedeckter kugelförmiger Skelettrest, dessen verhältnismässig grosse Exemplare in Marinen, die kleineren in Brackwasser-Schichten vorkommen».

Localité: Csákvár, sondage No 11, 131,9 m, dans la couche du Pannonien inférieur.

Monaxon, Oxea I.

Planche X, Fig. 5

Fragment lisse d'un spicule allongé, tubulé, s'amincissant au bout en pointe d'aiguille. Longueur: 57 μ, largeur 10 μ, diamètre du tube 1 μ.

Localité: Csákvár, sondage No 11, à 132,2 m, dans la couche du Pannonien inférieur.

Oxea II.

Planche X, Fig. 6

Fragment arqué d'un spicule en forme d'épine tubulaire, se rétrécissant au bout en pointe d'aiguille. La paroi du canal est épaisse, mais s'amincit en proportion du rétrécissement du diamètre. Longueur: 114 μ, largeur: 8 μ, diamètre du tube: 2,5 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Acanthostyl I.

Planche X, Fig. 7—8

Débris fragmentaire d'un spicule arqué, tubulaire, portant à la surface des épines dispersées. Longueur: 78 μ, largeur: 15 μ, hauteur des épines proéminentes: 3—5 μ. Le tube — par rapport à l'épaisseur du spicule — se trouve très étroit, le diamètre en est 1 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Acanthostyl II.

Planche X, Fig. 12

Fragment d'un spicule allongé à canal mince, et d'épines. Les épines proéminentes sont clairsemées, s'élévant au-dessus de la surface à peine de 2—3 μ. Chaque épine a son canal. Longueur du fragment: 70 μ, largeur: 14 μ.

Localité: Csákvár, sondage No 31, de 256,0 à 256,9 m, dans la couche du Pannonien inférieur.

Acanthostyl III.

Planche X, Fig. 10—11

Fragment d'un spicule épais, un peu courbé, au bout arrondi, surface verrucifère, tout en étant couverte de fines épines, canal étroit. Les petites

Tableau 2

Csv. 11.: 130,0 m; 131,9 m; 132,2 m; * 184,6–186,0 m — Csv.9.: 126,6–127,7 m; 144,5 m — Csv. 31.: 256,0–256,9 m; 256,9–261,7 m; 262,5–265,0 m

FOSSILIAE:	Écologie
Chrysophyta:	
Archaeomonas sphaerica Defl.	p.,+P.
Archaeosphaeridium ornatum Defl.	p.,● P.
Archaeosphaeridium cavernosum n.sp.	p.,+P.
Pararchaeomonas cariosa n.sp.	p.,+ P.
Chrysostomum sphaericum Hajós	p.,+ l.,M.
Outesia deflandreiana n.sp.	p.,+, S.
Bacillariophyta:	
Melosira granulata (Ehr.) Ralfs	p.,h.,e.,●,O.
Melosira granulata (Ehr.) Ralfs var. *pannonica* n. var.	p.l.,+,O,en.
Melosira cfr. *distans* (Ehr.) Kütz. var. *lirata* (Ehr.) Bethge	p.,l.,s.,●, O.
Melosira sol. (Ehr.) Kütz.	p., l.,●, P.
Melosira sp.	+, O.
Coscinodiscus jambori n.sp.	p.,l.,+, M.
Coscinodiscus jambori n.sp. f. *magna* n.f.	p.,l.,+, M.
Coscinodiscus jambori n.sp. f. *biseriata* n.f.	p.,l.,+, M.
Coscinodiscus jambori n.sp. f. *minor* n.f.	p., l.,+ M.
Coscinodiscus parvus n.sp.	●,l.,+ M.
Coscinodiscus lacustris Grun.	p.,l., h., ●, M
Coscinodiscus oculus-iridis Ehr.	p., pl., ●,P.
Actinoptychus senarius (Ehr.) Ehr.	p.,n.,eu,●,P.
Actinoptychus senarius (Ehr.) Ehr. var. *tamanica* (Jousé) Hajós	p.,n.,eu.,+, P.
Actinoptychus trilobatus n.sp.	p.,l.,+, M.
Licmophora abbreviata Ag.	l.,ep., ●, P.
Glyphodesmis distans (Greg.) Grun.	p.,l., ●, P.
Opephora martyi Hérib.	p.,l.,e.,eu.,● O.ph.7-9
Fragilaria construens (Ehr.) Grun.	l.,e.,m.,eu.,●,O
Fragilaria brevistriata Grun.	p.,li., ●,S.
Fragilaria brevistriata Grun. f. *elliptica* Hérib.	p.,h.,li.,●,S.
Fragilaria lapponica Grun.	p.,li.,●,S.
Fragilaria esthereia n.sp.	p.,l.,+, M.
Synedra sp.	+, M.
Cocconeis scutellum Ehr. var. *minutissima* Grun.	l.,ep., ●, M.
Cocconeis disculoides Hust.	l.,ep., i., ●, M.
Cocconeis placentula Ehr. var. *klinoraphis* Geitl.	l.,e.,eu.,ep.,●,O.
Cocconeis placentula Ehr. var. *lineata* (Ehr.) Cl.	l.,m.,i.,ep.,●,O
Cocconeis placentula Ehr. var. *intermedia* (Hérib & Perag) Cl.	l.,m.,i.,ep.,●,O
Cocconeis sp.	ep.,+, O
Achnanthes delicatula (Kütz.) Grun	l.,eu.,ep.,●,O
Achnanthes lanceolata (Bréb.) Grun.	l.,i.,ep., ●,S.
Mastogloia tuscula (Ehr.) n.comb.	l.,ep.,●, O.
Diploneis mauleri (Brun) Cl.	b.,li., ●, S.
Diploneis soói n.sp.	b.,l.,+ M.
Diploneis ovalis (Hilse) Cl.	b.,h.,ae.,●, M.
Stauroneis smithii Grun.	p.,l.,i., ●,O.
Navicula sp.	+ M.
Coloneis sp. I.	l., b.,+, M.
Coloneis sp. II.	l.,b.,+, M.
Epithemia salina Pant.	h.,+ O.
Nitzschia sp. I.	b.,l.,+, M.
Nitzschia sp. II.	b.,l.,+ M.
Surirella oblongella n.sp.	l.,+, M.,en.
Phytolitharia:	
Lithodontium	+,M.
Ciliata:	
Tintinnidium ? sp.	h.,l.,+, M.
Porifera:	
Monaxon; oxea	M.
Monaxon; acanthostyl	M.
Sphaeraster	M.

- - - rarus
— accessorius
▬ subdominans
■ dominans

P = polyhaline (Salinité de 20 à 40 ‰)
M = mésohaline (Salinité de 5 à 20 ‰)
O = oligohaline (Salinité de 0,02 à 5 ‰)
S = eau douce
+ = disparu
● = récent
* = sarmatien superieur

p = planctonique
ep = épiphyte
b = benthonique
pl = pélagique
n = néritique
l = littoral
li = limnique

h = halophile
eu = euryhaline
i = ubiquiste
e = eutrophe
m = mésotrophe
en = endémique
ae = aérophile

épines s'élèvent à peine de 1—2 μ au-dessus de la surface, mais elles sont très serrées. La longueur du fragment: 85 μ, largeur: 12 μ, diamètre du tube: 0,3 μ.

Localité: Csákvár, sondage No 11, 132,2 m, dans la couche du Pannonien inférieur.

Acanthostyl IV.

Planche X, Fig. 9

Spicule fragmentaire, allongé, tubulaire. La surface porte de petites épines clairsemées, chacune également tubulaire, bien que leur hauteur ne dépassent pas 1—2 μ. Longueur du fragment: 85 μ, largeur: 8 μ, diamètre du canal: 0,75 μ.

Localité: Csákvár, sondage No 11, 130,0 m, dans la couche du Pannonien inférieur.

IV.

Les données paléo-écologiques, concernant les taxons de l'association microflorique ainsi que les conditions de la sédimentation, ont été présumées d'après les données des espèces des mêmes associations existant aussi aujourd'hui. Surtout fallait-il prendre en considération la période du Pannonien inférieur dans le Bassin de Hongrie, et la aussi, premièrement les données et les résultats obtenus d'après la détermination des Mollusques. Selon les géologues, M. le Dr. ÁRON JÁMBOR (1970) — de l'Institut Géologique de Hongrie et M. KÁLMÁN TÓTH, de l'Entreprise de Recherches de Bauxite, à Balatonalmádi, les sédiments diatomiques traités ci-dessus renferment comme Mollusques caractéristiques que l'on y rencontre: *Didacna subdeserta* (Lőr), *Paradacna* cf. *lenzi* (R. Hoern.), *Limnocardium andrusovi* Lőr., *Limnocardium apertum* Münst., *Parvidacna tinnyeana* (Lőr.), *Congeria cžjzeki* M. Hörn. et *Congeria partschi* Cžjžek, dont l'espèce dominante est *Parvidacna tinnyeana*. M. FERENC BARTHA (1971), en analysant le biofaciès des sédiments pannoniens du Bassin de Hongrie, a signalé cette période de sédimentation peu saline comme produisant un faciès proche à la rive.

Le diagramme récapitulatif, concernant la fréquence et l'écologie des associations (Tableau 2) nous suggère à admettre que les couches diatomiques du Pannonien inférieur (sondages No 9, 11 et 31) de Csákvár proviennent, dans leur ensemble, de conditions paléogéographiques identiques, ou presque identiques. Concernant les conditions de sédimentation, on ne peut supposer de différences essentielles, ni d'après l'analyse quantitative ni d'après les espèces de la microflore. Le pourcentage écologique de la répartition par échantillons se trouve dans le Tableau 3; aussi les Figures 7 à 9 (diagramme en bloc) le présente.

Le pourcentage sommarisé des valeurs par échantillons est porté sur le Tableau 3, est sur les diagrammes 10 à 12.

Tableau N° 3

Les biofaciès des associations microfloriques, en pourcentage par couches, dans les sondages de Csákvár 9., 11. et 31

N° du sondage	Eau douce Oligohalin	Mésohalin	Polyhalin	Lacustre Fluviatil	Littoral	Néritique	Pélagique	Placnton	Épiphyte Sessile	Benthique
	%			%				%		
Csv. 11. 130.0 m	—	100.0	—	—	100.0	—	—	100.0	—	—
Csv 11. 131.9 m	14.3	85.7	—	14.3	85.7	—	—	100.0	—	—
Csv. 11. 132.2 m	25.0	75	—	12.5	87.5	—	—	87.5	12.5	—
Csv. 11.* 184.6–186.0 m	9.1	72.7	18.2	9.1	72.7	9.1	9.1	81.8	9.1	9.1
Csv. 9. 126.6–127.7 m	14.3	78.6	7.1	14.3	71.4	14.3		78.6	14.3	7.1
Csv. 9. 144.5 m	—	83.3	16.7	—	100	—	—	83.3	16.7	—
Csv. 31. 256.0–256.9 m	9.5	90.5	—	9.5	81	9.5	—	76.2	14.3	9.5
Csv. 31. 256.9–261.7 m	—	100	—	—	100	—	—	100	—	—
Csv. 31. 262.5–265.0 m	22.2	77.8	—	22.2	77.8	—	—	77.8	22.2	—
Données sommarisées, en pourcentage, des biofaciès des couches à Diatomées.	17.0	71.5	11.5	11.5	80.0	5.7	2.8	62.9	28.6	8.5

Csv. = Csákvár, * Sarmatien supérieur

En nous basant sur ces données, il est à constater que ce territoire appartenait à une zone peu profonde, tout près de la rive, car 80% des espèces sont littorales; puis 57% néritiques, et il n'y a que 2,8% qui soient pélagiques, venant du large, transportées et enlavées par les houles. Les spécimens pélagiques sont pour la plupart fragmentaires.

La proximité de la côte se déclare par la prédéposant tout près des côtes nous suggère la probabilité d'une réaccumulation par une mer agitée. Cela se montre possible par le fait que les formes planctoniques de grande dimension et à frustule délicate (*Actinoptychus trilobatus*) se retrouvent ici pour la plupart en fragments, tandis que les espèces à frustules épaisses (p. ex. *Coscinodiscus jambori*) sont intactes.

Le changement paléo-écologique le plus significatif de la mer pannonienne inférieure fut qu'elle commençait à perdre de sa salinité; l'association
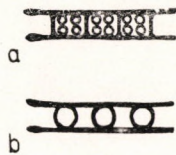
Fig. 6
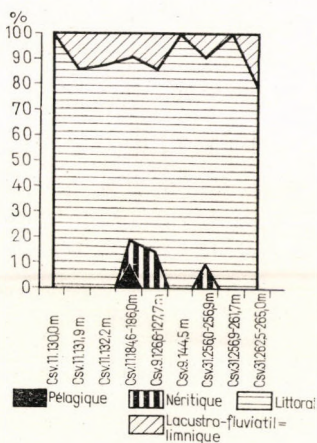
Fig. 7
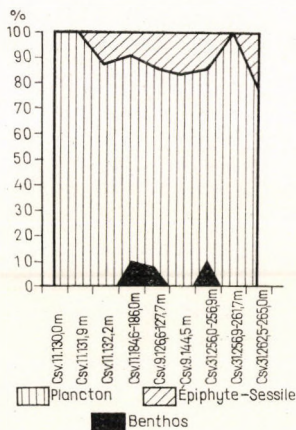
Fig. 8
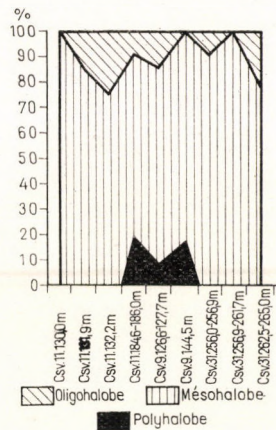
Fig. 9
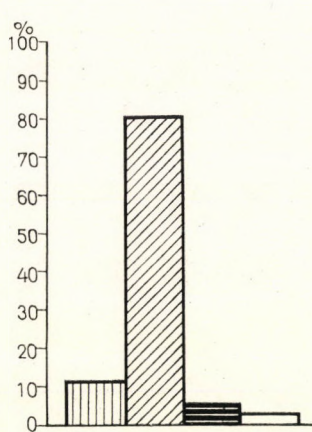
Fig. 10
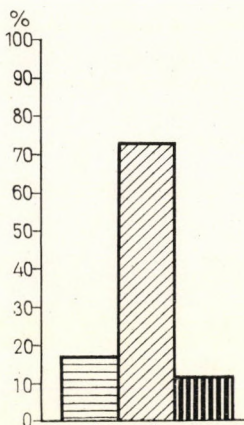
Fig. 11
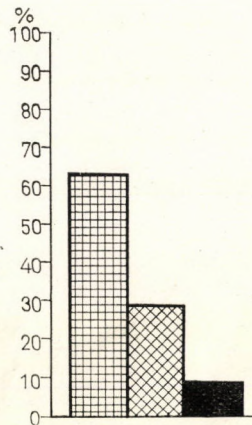
Fig. 12

des vestiges reflètent très nettement l'adoucissement des eaux de la baie d'autrefois surtout si l'on regarde les espèces selon la répartition en pourcentage de leur exigence en salinité. D'après le classement de KOLBE (REMANE, A.: 1958. p. 6. Abb. 2) 71,5% des espèces sont mésohalines; 17% oligohalines; et seulement 11,5% polyhalines. Si nous voulons comparer cette proportion avec la situation paléogéographique de l'étage du Pannonien inférieur, alors nous avons à observer que les sédiments diatomiques se produisent dans la période où les eaux commencent à perdre de leur salinité et montrent une oscillation tendant vers l'adoucissement. Ce fait est montré dans le Tableau 2 où les espèces énumérées, leurs variations et les variations morphologiques en sont témoins. Par exemple, parmi les formes *Centricae* l'espèce *Coscinodiscus jambori* présente l'allongement du disque dans le sens de l'axe longitudinal et la disposition des aréoles se modifie également en cette direction. C'est la diminution de la salinité, et avec cela le changement de la pression osmotique qui a mené cette espèce à sa nouvelle forme adaptatrice et différenciée d'ordre plus élevé.

En ce qui concerne les *Pennatae*, avec l'adoucissement des eaux, c'est au contraire l'axe longitudinal qui se raccourcit; chaque bout allongé de la cellule se rétrécit et reçoit une petite «tête» — le milieu de la cellule s'évase en s'élargissant, comme chez *Fragilaria construens*, ou changent en formes triangulaires, comme: *Fragilaria leptostauron* var. *triangula*.

Il est remarquable que nos espèces provenant de la partie supérieure du Pannonien inférieur, et là aussi de la phase régressive et oscillative, elles ont la taille plus grande et l'ornementation plus différenciée que les espèces du Tortonien ou du Sarmatien dérivant desquelles-elles s'adaptaient aux conditions écologiques changées.

Tout le complexe à Diatomées se caractérise par la forme planctonique dominante de *Melosira granulata* et sa variété, espèces dont les spécimens ont gardé leur chaînes à plusieurs cellules, même après la préparation. Il est donc à croire que le récipient du dépôt a dû être une baie littorale isolée dont le voisinage tout proche de la côte a prédisposé l'adoucissement de ses eaux. Mais c'est l'*Actinoptychus trilobatus* qui est vraiment caractéristique dans les couches étudiées et — étant vérifiée par macrofaune — elle est marqueur d'âge et de faciès. Cette espèce montre une affinité avec l'*Actinoptychus senarius* (espèce marine) mais il est à supposer que notre spécimen est une variété montrant l'adaptation au changement de la salinité des eaux. Jusqu'à présent nous ne l'avons connue que dans les sédiments diatomiques de la fin du Sarmatien et dans le Pannonien inférieur, à Tállya.

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NEUE CHLOROCOCCALEN AUS DEN ABSETZ- UND GRUNDWASSERANREICHERUNGSBECKEN DER BUDAPESTER WASSERWERKE

Von

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(Eingegangen am 20. Januar 1972)

Survey of 20 new taxa from basins of the Budapest Waterworks, fed with Danube waters. Between them were to be found 7 species, 3 varieties, 10 forms. The collections have been made in 1968—1969. At the times of the examinations the pH value was of 7,48—8,98, waterdepth of 70—120 cm. A more detailed description of the physical, chemical and limnologycal conditions is to be found in my paper »Mikroflora der Absetz- und Grundwasseranreicherungsbecken der Hauptstädtischen (Budapester) Wasserwerke«, published in the Revue of Hydrology ,,Hidrológiai Közlöny'' **50**, pp. 481—484, Budapest, 1970.

New taxa published: *Chodatella budapestinensis* Hortob., *Elakatothrix gracilis* Hortob., *Micractinium crassisetum* Hortob., *Oocystidium polymammilatum* Hortob., *Quadricoccus ellipticus* Hortob., *Tetrastrum parallelum* Hortob., *Tetrastrum tenuispinum* Hortob.

Chodatella budapestinensis Hortob. var. *trisetigera* Hortob., *Crucigenia truncata* G. M. Smith var. *scutata* Hortob., *Scenedesmus denticulatus* Lagerh. var. *disciformis* Hortob.

Chodatellopsis elliptica Korsch. f. *undulata* Hortob., *Lagerheimia trigona* Hortob. f. *longispina* Hortob., *Lagerheimia wratislawiensis* Schroed. f. *gracilis* Hortob., *Pediastrum Boryanum* (Turp.) Menegh. f. *flexuosum* Hortob., *Pediastrum duplex* Meyen var. *gracillimum* W. et W. f. *danubiale* Hortob., *Pediastrum tetras* (Ehr.) Ralfs var. *tetraodon* (Corda) *Hansg.* f. *globosum* Hortob., *Tetraëdron caudatum* (Corda) Hansg. var. *incisum* Lagerh. f. *punctato-flexocaudatum* Hortob., *Scenedesmus decorus* Hortob. var. *bicaudatus* Hortob. f. *heterogranulatus* Hortob., *Scenedesmus ellipsoideus* Chod. var. *bicaudatus* Hortob. et Németh f. *granulatus* Hortob., *Scenedesmus intermedius* Chod. var. *bicaudatus* Hortob. f. *danubialis* Hortob.

Von den mit Donauwasser gespeisten Becken mache ich 20 neue Taxa in meiner Arbeit bekannt. Davon sp. 7, var. 3, f. 10. Die Sammeln fanden in 1986—1969 statt. Während der Untersuchungen schwankte der pH-wert von 7,48 bis 8,98. Die Wassertiefe des Absetzbeckens messt 120 cm, die des Grundwasseranreicherungsbeckens 70 cm. Die Wassertemperatur ist im Grundwasseranreicherungsbecken höher als die im Absetzbecken; die Wasserbewegung verlangsamt sich wesentlich im Grundwasseranreicherungsbecken, auch seine Lebenswelt ist reicher. Mit den physikalischen, chemischen, und limnologischen Verhältnissen der Becken beschäftige ich mich ausführlicher in meiner Abhandlung: Mikroflora der Absetz- und Grundwasseranreicherungsbecken der Hauptstädtischen (Budapester) Wasserwerke (1970).

Die veröffentlichten Taxa: *Chodatella budapestinensis* Hortob., *Elekatothrix gracilis* Hortob., *Micractinum crassisetum* Hortob., *Oocystidum polymammilatum* Hortob., *Quadricoccus ellipticus* Hortob., *Tetastrum tenuispinum*

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Hortob.; *Chodatella budapestinensis* Hortob. var. *trisetigera* Hortob., *Crucigenia truncata* G. M. Smith var. *scutata* Hortob., *Scenedesmus denticulatus* Lagerh. var. *disciformis* Hortob., *Chodatellopsis elliptica* Korsch. f. *undulata* Hortob., *Lagerheimia trigona* Hortob. f. *longispina* Hortob., *Lagerheimia wratislawiensis* Schroed. f. *gracilis* Hortob., *Pediastrum Boryanum* (Turp.) Menegh. f. *flexuosum* Hortob., *Pediastrum duplex* Meyen var. *gracillimum* W. et W. f. *danubiale* Hortob., *Pediastrum tetras* (Ehr.) Ralfs var. *tetraodon* (Corda) Hansg. f. *globosum* Hortob., *Tetraëdron caudatum* (Corda) Hansg. var. *incisum* Lagerh. f. *punctato-flexocaudatum* Hortob., *Scenedesmus decorus* Hortob. var. *bicaudatus* Hortob. f. *heterogranulatus* Hortob., *Scenedesmus ellipsoideus* Chod. var. *bicaudatus* Hortob. et Németh f. *granulatus* Hortob., *Scenedesmus intermedius* Chod. var. *bicaudatus* Hortob. f. *danubialis* Hortob.

Beschreibung der neuen Taxa

1. **Chodatella budapestinensis** Hortob. n. sp.

Es wurde von mir schon aus Indien unter Namen *Chodatella* sp. veröffentlicht (1969, p. 38, Fig. 168). Zellen in Vorderansicht elliptisch, in Oberansicht rundförmig. In Kreuztform liegende vier Stacheln gerade, oder leicht gebogen, nadelspitz. Länge 4,7 bis 17 μ. Zellgrösse 6,5 bis 9×3,5 bis 5,2 μ. Chloroplast ein, wandständig, Pyrenoid gut sichtbar.

Nicht selten Juli—Oktober.

Konvergente Form von *Lagerheimia wratislaviensis* Schroed.

2. **Chodatella budapestinensis** Hortob. var. **trisetigera** Hortob. n. var.

Zellen elliptisch, Pole mitunter leicht bucklig, in Oberansicht mit rundem Durchschnitt. Zelldimensionen 7 bis 8×3,4 bis 4 μ. An den Polen je 1 gerader oder leicht gebogener, spitzer Stachel, um die Zellmitte 3 ähnliche Stacheln. Stachelnlänge 9,5 bis 18,2 μ. Chloroplast eines, parietal, Pyrenoid gut sichtbar.

Nicht selten.

Fig. 1. Chodatella budapestinensis Hortob. n. sp.
Fig. 2—3. Chodatella budapestinensis Hortob. var. *trisetigera* Hortob. n. var.
Fig. 4. Chodatellopsis elliptica Korsch. f. *undulata* Hortob. n. f.
Fig. 5—6. Crucigenia truncata G. M. Smith var. *scutata* Hortob. n. var.
Fig. 7—10. Elakatothrix gracilis Hortob. n. sp.
Fig. 11. Lagerheimia trigona Hortob. f. *longispina* Hortob. n. f.
Fig. 12. Lagerheimia wratislawiensis Schroed. f. *gracilis* Hortob. n. f.

Entschpricht der Alge von *Lagerheimia wratislaviensis* Schroed. var. *trisetigera* G. M. Smith.

Die *Ch. budapestiensis* und var. *trisetigera* konnte ich nicht in *Lagerheimia* genus einzureihen, da ihr Stachelbasis sich nie halbkugelförmig verdickte. Auch die beiden Chodatellen konnte ich nicht für junge Lagerheimien halten; die niedrigsten Grössen sind in beiden Genera gleich, sie kommen beisammen vor, aber infolge ihrer halbkugelförmigen Stachelbasis sind sie bestimmt zu erkennen.

3. **Chodatellopsis elliptica** Korsch. f. **undulata** Hortob. n. f.

Zelle elliptisch, $19,5 \times 15,6$ μ gross. In der Polengegend 10—12 wellige, nadelspitze, 41,6—48 μ lange Stacheln.

Selten August.

Weicht von der Art durch wellige Stacheln ab.

4. **Crucigenia truncata** G. M. Smith var. **scutata** Hortob. n. var.

Zellen bilden 4-zellige Coenobien, bei ihrer Begegnung eine grosse Höhle ist zu sehen. Zellen berühren sich mit ihren 1/3—1/2 Teil, an den Polen charakteristische, trichterartige Einbuchtung. An den Polen gebogene, kammartige oder schildartige Verdickung, deren Oberfläche rauch. In parietaler Chloroplast ein gut entwickeltes Pyrenoid. Zellgrösse 5,2 bis $10,4 \times 4,5$ bis 6,5 μ.

Selten — September.

Weicht von G. M. SMITHS Alge durch schildartige, hinunterziehende, gebogene Verdickung unebener Oberfläche ab.

5. **Elakatothrix gracilis** Hortob. n. sp.

Zellen stockförmig, an Enden abgerundet, oder können etwas verdünnt werden. Zelldimensionen 5,3 bis $10,4 \times 1,3$ bis 1,5 μ. Paarweise sichtbar. Zellen werden durch lange, in feiner Spitze endende farblose Hülle geschützt, deren Länge 90 μ erreichen kann. Chloroplast ein, parietal, in dem 1 Pyrenoid gut wahrnehmbar. 1—4 Zellen in einer Hülle.

Nicht selten Juni—August. Im Muster von Juli waren viel zu finden. Zellform gleicht der *Elakatothrix gelatinosa* Wille Zelle, Hülle der *E. lacustris* Korsch. Weicht von beiden durch kleinere Zelldimension, und durch schlanke, spitze Hülle ab. Die stockartige, schwach verjüngende Zellen erinnern an *E. alpina* G. Beck, jedoch bei dieser ist die Stellung der Zellen anders, auch die Ausmasse weichen ab (G. BECK, 1926, p. 181). Zellform ähnelt wenig *E. biplex* (Nygaard) Hindák, aber die budapester Zellen sind bedeutend kleiner und schlanker, auch die Hülle besitzt anderen Aufbau (HINDÁK, 1962, p. 285).

6. **Lagerheimia trigona** Hortob. f. **longispina** Hortob. n. f.

Grösse der flachen Zelle 2,7 bis 3 × 5,2 bis 5,6 μ. Länge der nadelspitzen, geraden Stacheln beträgt 29 bis 39 μ. Auf den Basen mit linsenartiger Verdickung, an die Zellwand haftend.

Selten — September.

Weicht von der Art durch lange Stacheln ab.

7. *Lagerheimia wratislaviensis* Schroed. f. *gracilis* Hortob. n. f.

Zelldimensionen 6 bis 6,6 × 3 bis 3,3 μ. Bei Stachelentspringen sind die Wülste relativ hoch, gut sichtbar; Stachel gerade oder sehr leicht gebogen, nadelspitz, 22 bis 24 μ lang.

Weicht von Grundform durch kleineres Ausmass und verhältnismässig lange Stacheln ab.

Selten — September.

8. **Micractinium crassisetum** Hortob. n. sp.

Zellen kugelartig, stehen zu viert unregelmässig, Membran glatt, Durchmesser 5,5 bis 6,5 μ lang. Je Zellen 2—3 sehr kraftvolle, steife hohler Fortsätze; gerade 1,7 bis 2,6 μ breit, bei Basis graduell verdünnen, in Nadelspitz enden. Länge 24,7 bis 33,8 μ. Ein grosses Chloroplast parietal, wo Pyrenoid gut sichtbar. Vermehrung durch Autosporen.

Selten — Juli—August.

Fortsatz-Gestaltung erinnert auch an *Conococcus elongatus* Carter (Philipose, p. 108—109), aber auf den *Conococcus* Zellen befindet sich immer ein kraftvoller Fortsatz, während bei diesem Organismus je Zellen 2—3. Dort die Zellen regelmässig, in Ebene geordnet, bei diesem haufenartig. In Zellengrösse, Fortsatzlänge kein Unterschied.

Weicht von jeden *Micractinum* Taxa durch sehr kraftvolle Fortsätze ab. Jedoch steht *M. pusillum* am nächsten.

9. **Oocystidium polymammilatum** Hortob. n. sp.

Dimensionen der ovalen Zellen mit glatter Wand 9,7 bis 11 × 6,5 bis 9,3 μ, mit 1 oder 2 Chloroplasten, Pyrenoid gut sichtbar. Zellen einzeln zu finden, liegen in der Mitte der breiten, farblosen, stark mammilanen Hülle, deren Ausmass 32,5 bis 57 × 27,3 bis 52 μ.

Selten — Juli—September.

Weicht von *Oocystidium ovale* Korsch durch schlankere Zellgrösse, und wellige, farblose Hülle ab.

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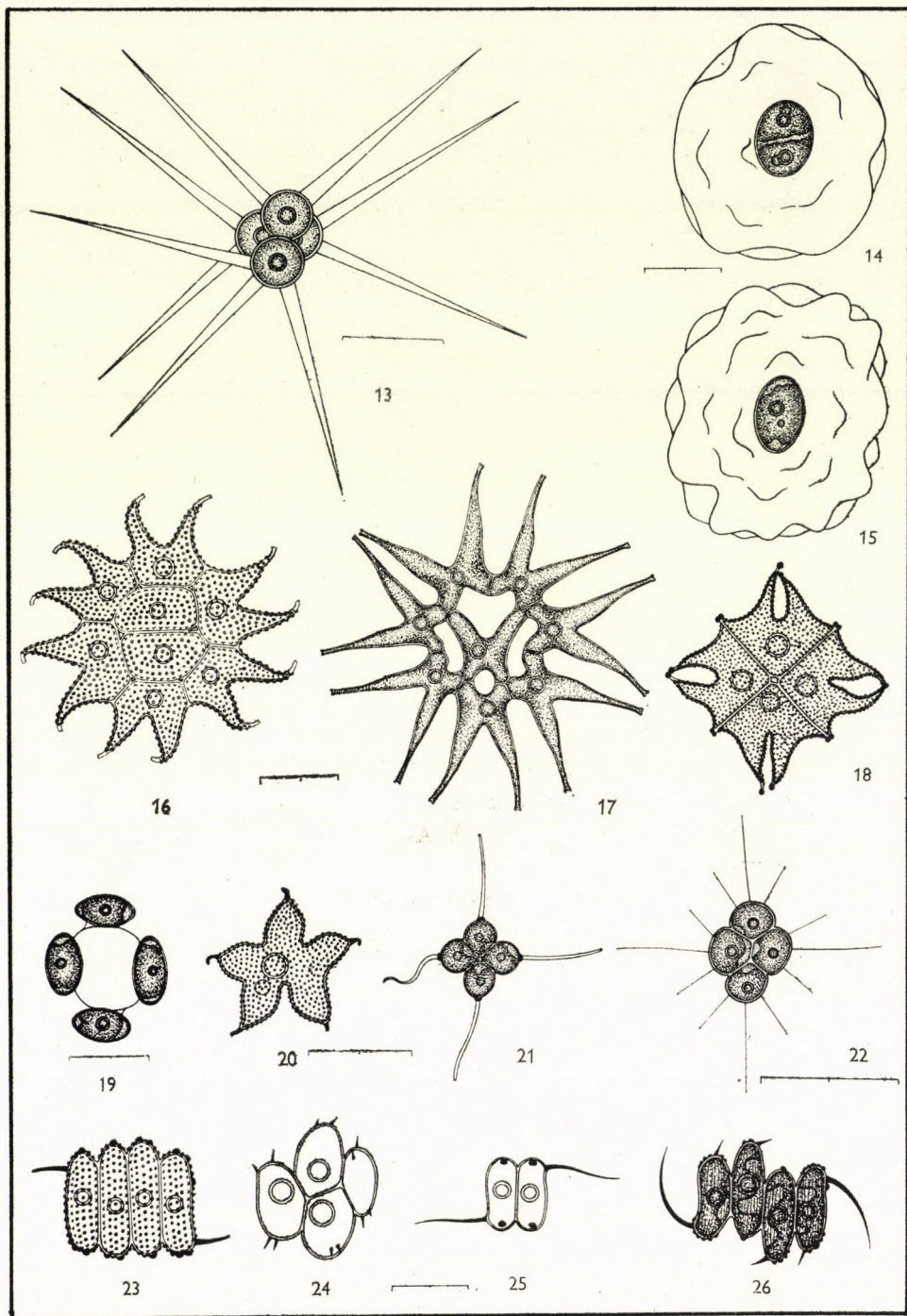
10. *Pediastrum Boryanum* (Turp.) Menegh. f. *flexuosum* Hortob. n. f.

Coenobien 8zellig, Zellgrösse 10,4 bis 12,2×10,4 bis 11 μ. Wände mit Wülsten bedeckt. Enden der Fortsätze biegen je Zellen stark in eine Richtung.

Selten — Oktober.

Weicht von den bekannten *P. Boryanum* Taxa durch gebogene Fortsätze ab.

11. *Pediastrum duplex* Meyen var. *gracillimum* *W.* et W. f. *danubiale* Hortob. n. f.

Coenobien 8zellig, Zellgrösse 9 bis 17×4 bis 5 μ, Membran glatt. Die Fortsätze der äusseren Zellen stark ausereinanderstehend, nicht gleichmässig dünn, sondern schinkenartig verdickt.

Selten — August—September.

Unterscheidet sich von var. *gracillimum* W. et W. durch typische verdickende Fortsätze.

12. *Pediastrum tetras* (Ehr.) Ralfs var. *tetraodon* (Corda) Hansg. f. *globosum* Hortob. n. f.

Bisher habe ich bloss 4zellige Coenobien beobachtet, Zelldimensionen 10—11×9 bis 10,3 μ. Membran mit winzigen Wülsten besetzt. An den Enden der Fortsätze gut sichtbare Kugeln.

Selten — August.

Weicht von der var. durch granulierte Membran, und durch die, an den Enden der Fortsätze ausbildenden Kugeln ab.

Fig. 13. Micractinium crassisetum Hortob. n. sp.
Fig. 14—15. Oocystidium polymammilatum Hortob. n. sp.
Fig. 16. Pediastrum Boryanum (Turp.) Menegh. f. *flexuosum* Hortob. n. f.
Fig. 17. Pediastrum duplex Meyen var. *gracillimum* W. et W. f. *danubiale* Hortob. n. f.
Fig. 18. Pediastrum tetras (Ehr.) Ralf var. *tetraodon* (Corda) Hansg. f. *globosum* Hortob. n. f.
Fig. 19. Quadricoccus ellipticus Hortob. n. sp.
Fig. 20. Tetraëdron caudatum (Corda) Hansg. var. *incisum* Lagerh. f. *punctato-flexocaudatum* Hortob. n. f.
Fig.. 21. Tetrastrum parallelum Hortob. n. sp.
Fig 22. Tetrastrum tenuispinum Hortob. n. sp.
Fig. 23. Scenedesmus decorus Hortob. var. *bicaudatus* Hortob. f. *heterogranulatus* Hortob. n. f.
Fig. 24. Scenedesmus denticulatus Lagerh. var. *disciformis* Hortob. n. var.
Fig. 25. Scenedesmus ellipsoideus Chod. var. *bicaudatus* Hortob. et Németh f. *granulatus* Hortob. n. f..
Fig. 26. Scenedesmus intermedius Chod. var. *bicaudatus* Hortob. f. *danubialis* Hortob. n. f.

13. **Qudricoccus ellipticus** Hortob. n. sp.

Zellen elliptisch-oval, Ausmass 7,2 bis 8×4 bis 4,6 μ. Zu viert, an Mutterzelle haften, Pole linsenartig verdickt, Membran glatt. Besitzen einen grossen, wandständigen Chloroplast, Pyrenoid gut sichtbar.

Selten — August—September.

Unterscheidet sich von durch Fott beschriebene *Quadricoccus ornatus* durch oval-elliptische Zellform, und durch Verdickung der Pole.

Im Ausmass ist mit *Q. laevis* Fott vollkommen identisch, die Zellen der Budapester sind aber elliptisch, und an den Polen linsenartig verdickt (FOTT, 1948, p. 9—11).

14. *Tetraädron caudatum* (Corda) Hansg. var. *incisum* Lagerh. f. *punctato-flexocaudatum* Hortob. n. f.

Zellwände mit kleinen Wülsten bedeckt. Zellgrösse mit Stacheln 14 bis 15×14,8 bis 15,6 μ. Stacheln dick, stump und stark gebogen, Länge höchstens 2 μ.

Weicht von var. durch stumpfe, dicke, stark gebogene, kurze Stacheln ab.

Selten — September—Oktober.

15. **Tetrastrum paralellum** Hortob. n. sp.

Durchmesser der Zellen 3,5 bis 4 μ, bei Treffen kleine Höhle. Am Pole jeder Zelle befindet sich eine Wulst, davon stammt der wenig oder stärker gebogene, kraftvolle, stumpf endende, 7 bis 8,5 μ lange Fortsatz. Zellen mit einem Chloroplast, in dem ein gut sichtbares Pyrenoid zu finden ist.

Selten — Juni.

Steht *Tetrastrum elegans* Playf. am nächsten.

Weicht von dieser durch Stachelbasis, und durch dickere, stumpfe Fortsätze ab.

Die über Stachelbasis verfügende Tetrastren erweisen sich ebenso solche paralelle Morphosen, wie z. B. die Erscheinung der Stachelbasis bei *Scenedesmus*-Arten. Es ist zu erwarten, dass auch die Taxa mit Stachelbasis der schon bekannten Tetrastren zum Vorschein kommen.

16. **Tetrastrum tenuispinum** Hortob. n. sp.

Die in derselben Ebene liegenden Zellen fügen sich lückenlos zueinander. Durchmesser 2,6 bis 3,2 μ lang. Je Zellen 3 Stacheln; der in der Achse liegende ist länger, den 6,3 bis 7 μ ist, daneben je 1 Stachel von Länge 3,7 bis 5 μ. Jeder Stachel sehr dünn, auch mit Phasenkontrast-Apparat schwer zu erblicken. Pyrenoid gut sichtbar.

Selten — September.

Steht der Alge *Tetrastrum triacanthum* Korsch. am nächsten, weicht von dieser durch sehr dünne Stacheln ab.

Die dick- und dünnstacheligen Taxa treten in *Tetrastrum*-Gattung als paralelle Morphosen auf. So ist *T. hastiferum* Korsch. das dünnstachelige Entsprechende von *T. elegans* Playf; *T. Péterfii* Hortob. (Hortobágyi, 1967. p. 42) entspricht *T. staurogeniaeforme* (Schroed.) Lemm. var. *longispinum* G. M. Smith; die jetzt beschriebenen Taxa entspricht der Alge *T. triacanthum* Korsch.

17. **Scenedesmus decorus** Hortob. var. **bicaudatus** Hortob. f. **heterogranulatus** Hortob. n. f.

4zellige Coenobien, Zellen liegen in derselben Ebene, gestreckte cilindrisch. Zelldimensionen 10,4 bis 11,8 × 3 bis 3,4 μ. Oberflächen werden mit Reihen kleinerer Wülste bedeckt, darunter befinden sich verstreut grössere Wülste. An Randzellen, bloss in einer Diagonale, befindet sich der gut entwickelte, stumpfe, etwas gebogene, auf die Zellen vertikal stehende 3,2 × 3,4 μ lange Stachel.

Selten — Juni—Juli, September.

Weicht von var. *bicaudatus* Hortob. durch winzige und grössere Wülste, stumpfe Stacheln, durch Mangel an winzigen Sacheln ab. Unterscheidet sich von f. *granulatus* Hortob. durch unregelmässig liegende grössere Wülste, stumpfe Fortsätze, durch Mangel an winzigen Stacheln.

18. *Scenedesmus denticulatus* Lagerh. var. **disciformis** Hortob. n. var.

Auch das zweireihige, lückenlose, s. g. disciformis Erscheinen der Zellen bildet paralelle Morphose. Die disciformis Figuren von diesem Typ haben die Verfasser innerhalb der Art bisher nicht abgesondert. Auf Grund der Donauer Untersuchungen finde ich motiviert, die über denticulate Stachelfigur, aber viel mehr stämmigere Zelle verfügenden, zweireihigen, zwischen den Zellen lückenlose Coenobien von den typischen denticulaten Coenobien zu unterscheiden.

Zellen gewöhnlich 4zellig, oval, mit stämmiger Form, die sich lückenlos aneinander passen. Zellwände nach auswärts breit wölbend. Membran glatt, Zellgrösse 8 bis 12 × 5 bis 7 μ. An beiden Polen der Randzellen je 2 nadelspitze. kurze Stacheln. An den freien Polen der Mittelzellen je 2 Stacheln von ähnlicher Grösse und Gestalt.

Weicht von der Art durch zweireihige Coenobien ab.

Nicht selten — Juli—September.

19. *Scenedesmus ellipsoideus* Chod. var. *bicaudatus* Hortob. et Németh f. *granulatus* Hortob. n. f.

Bloss 2zellige Coenobien kamen vor. Zelldimensionen 9 bis 9,5×3,8 bis 4,2 μ. Länge der Stacheln 7,8 bis 9 μ. An den Polen je ein gut entwickelte Wulst.

Selten — August.

Weicht von var. durch Wülste ab.

Hierher zu zählend sind die unter Namen *S. ellipsoideus* Chod. var. *bicaudatus* Hortob. veröffentlichten indischen Coenobien (HORTOBÁGYI, 1968, p. 59, Fig. 358—359). Die Vorigen in Acht nehmend modifiziert die Zellgrösse: 7,3 bis 11,7×3 bis 4,2 μ. Länge der Stacheln: 7,8 bis 9,5 μ.

20. *Scenedesmus intermedius* Chod. var. *bicaudatus* Hortob. f. *danubialis* Hortob. n. f.

4zellige Coenobien, Zellen kraftvoll alterniert, berühren sich mit Halbkörperlänge, Pole hoch gewölbt; Zellengrösse 10,4 bis 12,6×4 bis 4,6 μ. In einer Diagonale, an den Polen der Randzellen ein, den Zellen zu biegender, kraftvoller, spitzer, 10,4 bis 11 μ langer Stachel; an dem anderen Pol je 1 kurzer Stachel. An den stärker nach auswärts stehenden Polen der Mittelzellen ist je 1 ähnlicher Stachel zu beobachten. Länge dieser kurzen Stacheln beträgt 2 bis 2,5 μ. An den Zellpollen sitzen die kürzerer-längeren Reihe der kleiner-grösseren Wülsten. Auf Membran dünnes, abreissendes Stricheln. Auffallend, dass die Stacheln auf den Zellen des Coenobiums in Richtung des Ganges von Uhrzeiger stehen.

Selten — September.

Steht var. *bicaudatus* Hortob. f. *granulatus* Hortob. am nächsten. Weicht von dieser durch kleine Stacheln, in dieselbe Richtung blickende kleine und grosse Stacheln, sowie durch gestrichelte Membran ab.

Durch kleine Stacheln erinnert an var. *indicus* Hortob., aber jener hat keine Wulst, ferner andere Stachelstellung. (HORTOBÁGYI, 1968, p. 56—57, Fig. 369—370.)

Diagnosen

1. **Chodatella budapestinensis** Hortob. n. sp.

Cellulae a fronte ellipticae, superne circulares, 6,5—9×3,5—5,2 μ, spinis 4, in crucis formam ad polos et lateraliter dispositis, rectis, vel parum arcuatis, mucronatis, 4,7—17 μ longis, chloroplastide unico, parietali, pyrenoide distincto. — Jul.—Oct.

2. **Chodatella budapestinensis** Hortob. var. **trisetigera** Hortob. n. var.

Cellulae 7—8×3,4—4 μ, spina 1—1, acuta, in polis disposita, spinis similibus 3, in medio dispositis: rectis, vel parum arcuatis, 9,5—18,2 μ longis. — Jul.—Oct.

3. **Chodatellopsis elliptica** Korsch. f. **undulata** Hortob. n. f.

Cellulae 19,5—15,6 μ, spinis 10—12, undulatis, acutis, 41,6—48 μ longis, in polis dispositis. — Aug.

4. **Crucigenia truncata** G. M. Smith var. **scutata** Hortob. n. var.

Coenobia 4-cellularia, inter cellulas hiatu magno; cellulis 5,2—10,4×4,5—6,5 μ, parte 1/3—1/2 longitudinis sese attingentibus, in polis excavatione propria infundibuliformi incrassa-

tioneque arcuata, crista vel scuto simili, superficie verruculosa, pyrenoida bene evoluta unica, in chloroplastide parietali disposita. — Sept.

A specie incrassatione scutiformi, verrucosa polorum distincta.

5. **Elakatothrix gracilis** Hortob. n. sp.

Cellulae plerumque binae, baculiformes, versus apices late rotundatos forte tenuiescentes, 5,3—10,4×1,3—1,5 μ, chloroplastide unico, parietali pyrenoidave unica, distincta; 1—4 cellulae capsula communi, elongata, hyalina, usque ad 90 μ longa, apicibus mucronatim producta circumdatae. — Jun.—Aug.

6. **Lagerheimia trigona** Hortob. f. **longispina** Hortob. n. f.

Cellulae planae, 2,7—3×5,2—5,6 μ, spinis rectis, mucronatis, ad basin lentiformiter incrassatis, 29—39 μ longis ornatae. — Sept.

A specie spinis longis distincta.

7. **Lagerheimia wratislawiensis** Schroed. f. **gracilis** Hortob. n. f.

Cellulae 6—6,6×3—3,3 μ, spinis rectis, vel parum arcuatis, mucronatis, 22—24 μ longis verruculisque ad basin spinarum dispositis, pro ratione altis, conspicuis ornatae. — Sept.

A specie dimensione minore spinisve solito longioribus distincta.

8. **Micractinium crassisetum** Hortob. n. sp.

Cellulae quaternae, irregulariter dispositae, globosae, 5,5—6,5 μ diam., chloroplastidibus singulis, parietalibus, pyrenoida conspicua, pro cellula 2—3 spinis, rectis, rigidis, cavernosis, crassissimis, gradatim tenuiescentibus, mucronatis, 24,7—33,8 μ longis, ad basin 1,7—2,6 μ crassis. Propagatio per autosporas. — Jul.—Aug.

Ab omnibus *Micractinium*-taxonibus spinis crassissimis distinctum.

9. **Oocystidium polymammilatum** Hortob. n. sp.

Cellulae ellipsoidicae, leves, 9,7—11×6,5—9,3 μ, solitariae, chloroplastidibus 1—2, pyrenoide conspicuo, in medio capsulae hyalinae, valde mammilatae, 32,5—57×27,3—52 μ magnitudinis dispositae. — Jul.—Sept.

Ab *Oocystidio ovali* Korsch. dimensione graciliore capsulave hyalina, undulata distinctum.

10. **Pediastrum Boryanum** (Turp.) Menegh. f. **flexuosum** Hortob. n. f.

Cellulae 10,4—12,2×10,4—11 μ, membrana papillosa, apicibus processuum in eandem partem valde inclinatis. — Oct.

A *Pediastrum boryanum*-taxonibus processibus inclinatis distinctum.

11. **Pediastrum duplex** Meyen var. **gracillimum** W. et W. f. **danubiale** Hortob. n. f.

Cellulae 9—17×4—5 μ, membrana levi, processibus cellularum extimarum valde distantibus, ad formam pernarum incrassatis. — Aug.—Sept.

A var. *gracillimo* processibus proprie incrassatis distinctum.

12. **Pediastrum tetras** (Ehr.) Ralfs var. **tetraodon** (Corda) Hansg. f. **globosum** Hortob. n. f.

Cellulae 10—11×9—10,3 μ, membrana papillis parvis cooperta, in apicibus processuum globulis applicatis. — Aug.

A var. membrana granulata globulisve in apicibus processuum applicatis distinctum.

13. **Quadricoccus ellipticus** Hortob. n. sp.

Cellulae ellipticae-ovales, 7,2—8×4—4,6 μ, membrana levi, polis lentiformiter incrassatis, chloroplastide parietali, pyrenoida instructo. — Aug.—Sept.

Qu. ornato Fott procimus, ab eo forma cellularum incrassationeve polorum distinctus.

14. **Tetraëdron caudatum** (Corda) Hansg. var. **incisum** Lagerh. f. **punctato-flexocaudatum** Hortob. n. f.

Cellulae 14—15×14,8—15,6 μ, (spinis additis), spinis crassis, obtusis, valde inclinatis, ad summum 2 μ longis, membrana papillis parvis cooperta. — Sept.—Oct.

A var. spinis obtusis, crassis, brevibus, valde inclinatis distinctum.

15. **Tetrastrum parallelum** Hortob. n. sp.

Cellulae 3,5—4 μ diam., chloroplastide unico parietali pyrenoidave unica instructae; inter eas in medio hiatus parvus. In polo uniuscuisque cellulae processus singuli, crassi, obtusi, inclinati, 7—8,5 μ longi, e papilla orti. — Jun.

Tetrastro eleganti Playf. simile, sed parte basali papilliformi processuum, processibusque obtusis, crassioribus distinctum.

16. **Tetrastrum tenuispinum** Hortob. n. sp.

Cellulae diam. 2,6—3,2 μ, in uno plano, sine hiatu compositae, chloroplastide unico, pyrenoida conspicua instructae; cellulae omnes spinis ternis, tenuissimis: una earum media, secundum axem cellulae disposita, 6,3—7 μ longa, bifaria spina 1—1, longitudine 3,7—5 μ. — Sept.

A *T. triacantho* Korsch. spinis tenuioribus distinctum.

17. **Scenedesmus decorus** Hortob. var. **bicaudatus** Hortob. f. **heterogranulatus** Hortob. n. f.

Cellulae 10,4—11,8 × 3—3,4 μ, superficie seriebus granulorum parvorum inter eas sparse granulis majoribus cooperta. Spinae cellularum extimarum secundum unum diagonalem evolutarum 3,2—3,4 μ longae. — Jun.—Jul. Sept.

A var. *bicaudato* Hortob. granulis parvis atque majoribus, spinis obtusis, atque inopia spinarum parvarum; a f. *granulato* Hortob. granulis majoribus inordinate dispositis, processibus obtusis inopiave spinarum parvarum distinctus.

18. **Scenedesmus denticulatus** Lagerh. var. **disciformis** Hortob. n. var.

Coenobia e cellulis 8—12 × 5—7 μ, ovalibus, membrana levibus, biseriatim, sine hiatu composita. In polis ambobus cellularum extimarum spinae binae, mucronatae, breves in polis liberis cellularum mediarum spinae binae illis dimensione formave similes. — Jul.—Sept.

A specie coenobiis biseriatis distinctus.

19. **Scenedesmus ellipsoideus** Chod. var. **bicaudatus** Hortob. et Németh f. **granulatus** Hortob. n. f.

Cellulae 7,3—11,7 × 3—4,2 μ, spinis 7,8—9,5 μ longis, in polis 1—1 granulo bene evoluto ornatae. — Aug.

A var. *granulis* distinctus.

20. **Scenedesmus intermedius** Chod. var. **bicaudatus** Hortob. f. **danubialis** Hortob. n. f.

Cellulae 10,4—12,6 × 4—4,6 μ, valde alternantes, parte 1/2 longitudinis sese attingentes, polis serie granulorum majorum-minorum ornatis, alte convexis, membrana tenuiter, interrupte lineata. Poli cellularum extimarum 1—1 spina crassa, acuta, 10,4—11 μ longa, ad cellulas inclinata, secundum unum diagonalem tantum evoluta, secundum alterum diagonalem autem 1—1 spina 2—2,5 μ longa instructi; poli cellularum mediarum valde exstantes, 1—1 spina illis brevioribus simili ornati. — Sept.

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INVESTIGATION INTO THE 2,4-D EFFECT ON SOME METABOLISM INDICES IN VICIA FABA SEEDLINGS

By

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The roots of *Vicia faba* seedlings were treated with Dikonirt solution of a concentration (28 ppm) detrimental to the plant. Under treatment, the activity of the two important enzymes, viz. peroxidase and ascorbic acid oxidase, — which play a part in terminal oxidation — has increased. This process may be the consequence of oxidation in the reduced products in a way differing from the normal process of metabolism. The inhibition of pigment synthesis is shown by the decrease in total pigment content.

Introduction

In the course of our experiments we wanted to know how the quantity detrimental to plant tissue of 2,4-D (28 ppm) effects the activity of the two enzymes of terminal oxidation, viz. peroxidase and ascorbic acid oxidase. The detrimental effect exercised by 2,4-D on the root system manifests itself in the activation of enzymes participating in the oxidative processes, while other processes, e.g. the pigment synthesis, are inhibited. The aging of tissues and organs is accompanied by similar processes (KISBÁN et al. 1964, ROJIK et al. 1970, HORVÁTH—LASZTITY 1967).

Material and method

The experiments were performed with 5-day old *Vicia faba* seedlings in hydroculture pots. Part of the seedlings was put in a solution of 28 ppm concentration of the sodium salt of 2,4-dichlorophenoxi-acetic acid (Dikonirt) dissolved in tap-water, while the other part as control was placed in tap water. The pots were kept in a light thermostat (HORVÁTH—LASZTITY 1965); the solutions were changed every 2 days.

For the examinations samples were taken from the first day after treatment till the tenth day. Settings of the experiment and determinations were carried out 8—10 replications. The activity of ascorbic acid oxidase was measured according to the method of KIRÁLY and FARKAS (1957). Measuring of the peroxidase enzyme activity was accomplished on the basis of the guaiacol method of SOLYMOSY and FARKAS (1963). The quantity of ascorbic acid was established by titration with 2—6 dichlorphenol-indophenol. The determination of the total pigment content was done with the method reported by SMITH and BENITES (1963).

Results and discussion

The activity of peroxidase has been examined in the root and in the shoot. Under the effect of Dikonirt the enzyme activity increased per organ and it showed to be the greatest in the root of the plant treated.

Table 1

Effect of 2,4-D on the peroxidase enzyme activity of Vicia faba seedling
(Calculation: expressed in the percentage of the control leaf activity)

Treatment in days	Control		Treated	
	leaf	root	shoot	root
2	1.00	3.14	2.01	4.42
3	0.76	3.26	3.22	4.45
6	0.81	3.87	4.49	8.97
7	0.92	3.54	4.48	8.91
8	0.93	3.88	4.48	8.96

Ascorbic acid quantities gave similar results

Table 2

Effect of 2,4-D on the ascorbic acid content of Vicia faba seedlings
(Calculation: γ/g for fresh weight)

Treatment in days	Control		Treated	
	leaf	root	shoot	root
3	490	340	540	535
4	580	379	645	630
5	324	198	462	892
9	404	200	887	1193

Under the effect of treatment the activity of ascorbic acid oxidase increases. The activity for 1 g fresh weight decreases with the lapse of time.

Table 3

Effect of 2,4-D on the ascorbic acid oxidase activity of Vicia faba seedlings
(Calculation: O_2 intake in micro-liter for 1 g fresh weight (/hour)

Treatment in days	Control	Treated
3	118	138
4	74	132
9	18	122
10	6	86

According to the data of literature (HERRET—BERTHOLD, 1965) herbicides inhibit pigment synthesis. This occurred also with 2,4-D in our experiments.

Table 4

Effect of 2,4-D on the total pigment content of Vicia faba seedling

(Calculation: γ/mg fresh weight)

Treatment in days	Control	Treated
9	2.68	0.278
10	2.31	0.375

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ULTRASTRUCTURE INVESTIGATIONS OF ANGIOSPERMATOPHYTE POLLENS FROM THE LOWER EOCENE

By

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Further nine species have undergone ultrastructural investigations in the course of examinations of Angiospermatophyte pollen from the Lower Eocene. A new form-genus (*Transdanubiaepollenites*) and a new form-species (*Tricolporopollenites sooi*) described, and their ultrastructure also given. Of the form-species described formerly on the basis of optical microscopical investigations, the diagnoses of *Basopollis basalis* Pf. 1953, and of *Diporites iszkaszentgyörgyi* Kds 1965, are new complemented with electronmicroscopical data.

Introduction

In the previous studies (KEDVES and PÁRDUTZ 1970a, 1970b) the first results of ultrastructural investigations of the Angiospermatophyte pollen from the Lower Eocene (deposits of the Parisian Region) were given. The investigations were continued on further types of pollen grains from the same period, and the related new data are summarized in this study.

Material and method

The examined material was collected from the Lower Eocene deposits at Úrkút (Hungary) and from the formerly described locality of the Parisian Region (KEDVES and PÁRDUTZ 1970). Concurrently with the electronmicroscopical investigations, the optical microscopical study of the form-species were also made, wherever it was found necessary. When describing the new taxa, not only optical microscopical but also electronmicroscopical data are used in the diagnoses.

Results

Basopollis basalis (Pf. 1953a) Pf. 1953b

(1–6 in Plate I)

The specimen is from the Sparnatian deposits of the Parisian Basin.

TEM diagnosis

Extragerminal exine tectate, tectum segmented or transversed with narrow channels. Surface marked with spinules. Tectal depth largely equivalent to that of combined thickness of columellar layer and foot layer. Annulus forming columellar layer produces by multiple investigations a preavestibule along pore channel. Foot layer separating from columellar layer (vestibule).

Plate I. Basopollis basalis (Pf. 1953a) Pf. 1953b. 1, 2. Optical microscopical picture of embedded specimen examined ultrastructurally ×1000. 3. Section of germinal exine ultrastructure near pore region. ×5000. 4. Ultrastructure of germinal region. ×10 000. 5. Ultrastructure of germinal region. ×5000. 6. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer, sp = spinae, P = pore, Pv = praevestibulum, A = annulus, V = vestibulum

Electronmicroscopical results

Extragerminal exine.—Tectate, locally segmentate or transversed with very narrow channels. Surface with definite spinules. Columellar layer not invariably separate from tectum, its elements more or less column-shaped and densely arranged (6, Plate I). Lower part of foot layer with a section showing a stronger electron affinity. (This is probably an artificial product owing to the preparation technique of the material.)

Tectum slightly narrow in pore region than extragerminally (5, Plate I). Surface with spinules, channels more densely, than in extragerminal ectexine (3—5, Plate I). Columellar layer markedly separating from tectum, its elements multiple, thus layer here much thicker than in extragerminal region. Its ultrastructure consists of varying densely anastomosing elements (4, Plate I). Praevestibulum formed in pore channel (4, Plate I) by uneven investigations of columellar layer. Foot layer separating from columellar layer; this is the vestibulum by the ultrastructural data (4 and 5, Plate I).

The ultrastructure of the form-genus deviates from that of the Lower Eocene *Normapolles* investigated previously (KEDVES and PÁRDUTZ 1970). The narrow channels of the tectum, but especially the columellar layer of the extragerminal exine, deviate from that of the form-genera *Pompeckjoidaepollenites* (Pf. 1953b) W. Kr. 1967, *Nudopollis* Pf. 1953b, and *Plicapollis* Pf. 1953b, where the columellar layer consits of spheroid or ellipsoidal elements; it is of *Myricaceae/Juglandaceae* character. The data given by TAKEOKA and STIX (1963) concerning the recent *Amentiflorae*, *Betulaceae* exine ultrastructure, are similar to those of our pollen grain, although they do not perfectly correspond to it. So our pollen is only assumably the pollen of an extinct *Amentiflorae* taxon.

Diporites iszkaszentgyörgyi Kds. 1965
(1—7 in Plate II; 1—3 in Plate III)

The material is from the Lower Eocene layers of Úrkút (Borehole No. U-218). Hundred specimens of the form-species were studied by the optical microscope.

TEM Diagnosis

Exine dividing into ectexine and endexine. Ectexine tectate, tectum perforated, elements of columellar layer various. Foot layer thicker than tectum under it endexine with lamellar ultrastructure constituting also pore membrane. Foot layer slightly thickening near pores and forming annulus.

Results by optical microscope

Twelve specimens of the examined material showed a pore membrane (1 and 2, Plate III). Pore eventually situated also within contour (3, Plate III); in this case pore membrane well observable if viewed from above. Pores of subequal dimensions within one pollen grain, diameter of a larger pore 6.5—15 μ (maximum 9—10—11 μ) that of smaller ones 6—14 μ (a marked maximum at 9 μ). Lenght of pollen grain 39—56 μ, its width 28—43 μ. Rate of length and width between 1.1—1.9.

Electronmicroscopical results

Extragerminal exine.—Tectate, perforate (2, Plate II); perforations mostly of irregular shape if viewed from above (6, Plate II). Elements of columellar layer variform; of a straight columnar, spheroid, or irregularly anastomosing shape. Foot layer thicker than tectum, T/C/F = 1.8—2/1/2—2.5, with occasionally an endexine of lamellar ultrastructure observable below it.
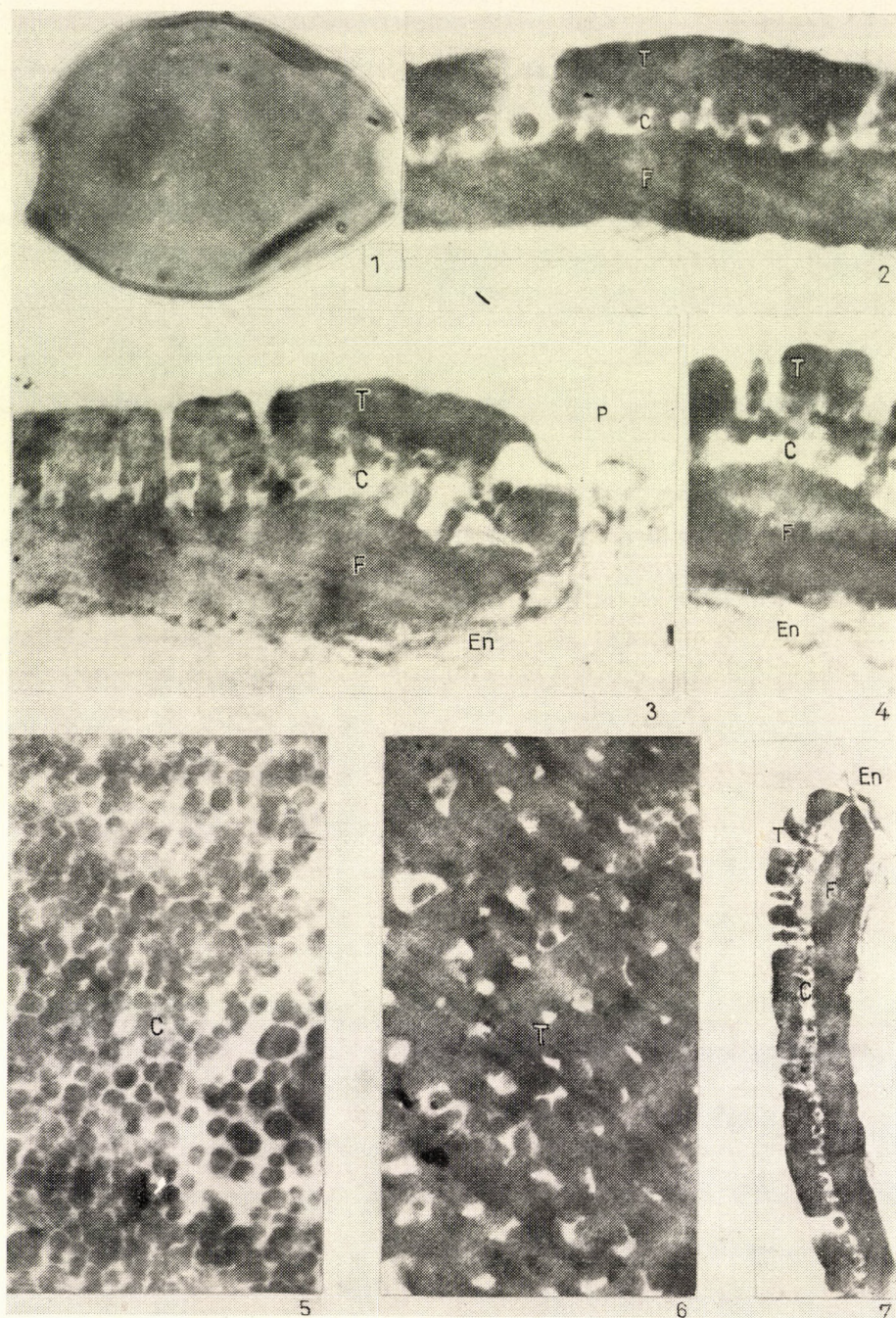
Plate II. Diporites iszkaszentgyörgyi Kds. 1965. 1. Optical microscopical picture of embedded specimen examined ultrastructurally. ×1000. 2. Section of extragerminal exine ultrastructure. ×25 000. 3, 4. Germinal region ultrastructure. ×25 000. 5. Tangential section of the columellar layer. ×25 000. 6. Tangential section of the tectum. ×25 000. 7. Ultrastructure of the pore region and the adjacent extragerminal exine. ×10 000. T = tectum, C = columellae, F = = foot layer, En = endexine
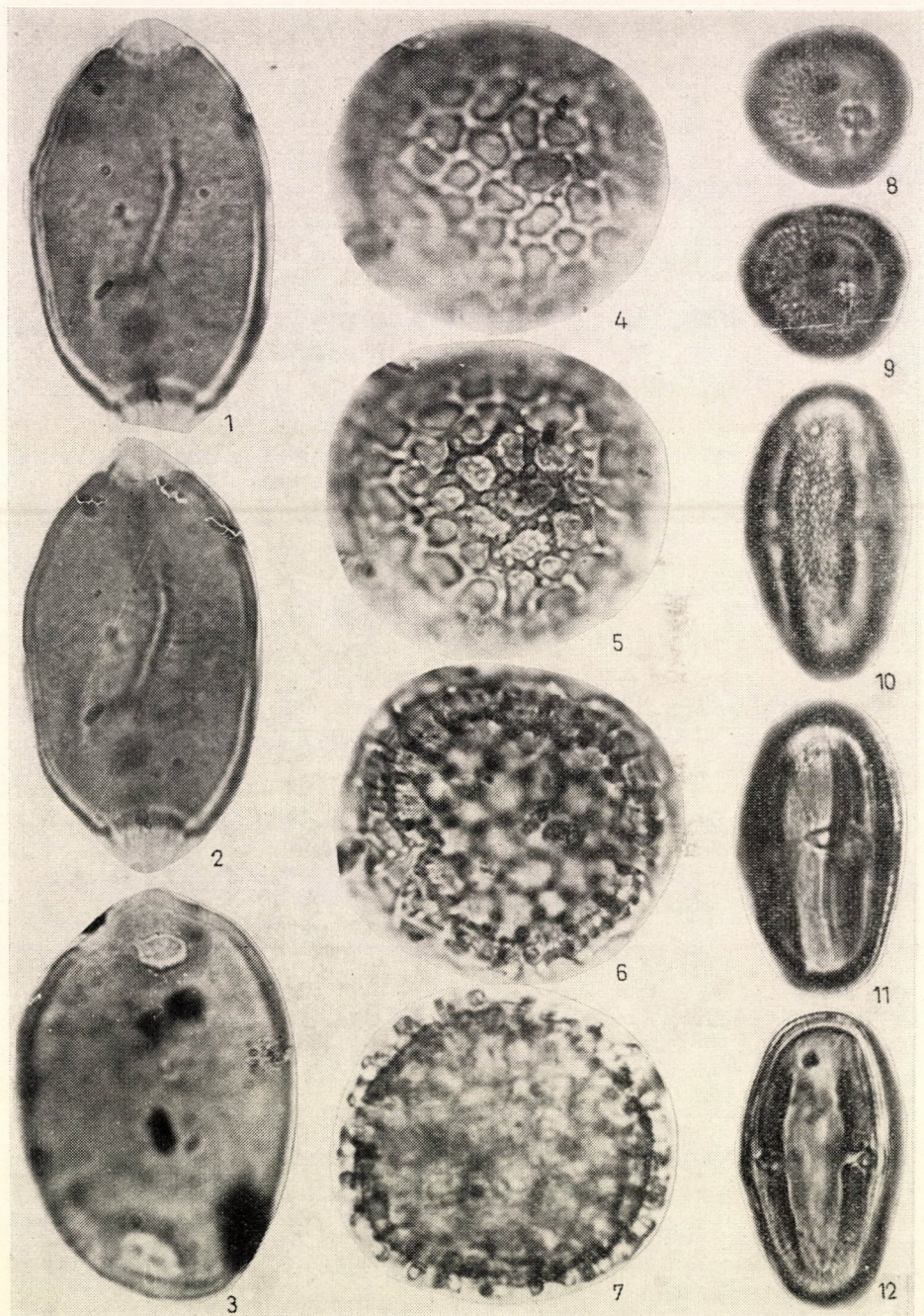
Plate III. 1. *Diporites iszkaszentgyörgyi* Kds. 1965, prep.: U-218-13-10, cross-table number 14. 7/110, 7. 2, 3. *Diporites iszkaszentgyörgyi* Kds. 1965, prep.: U-218-2-10, cross-table number: 20, 5/113, 6. 4—7. *Transdanubiaepollenites magnus* n. fgen. et fsp., *Nyctaginaceae*, prep.: U-218-13-9, cross-table number: 19, 2/117,5. 8, 9. *Tricolporopollenites sooi* n. fsp., *Pandaceae*, prep.: U-218-13-9, cross-table number: 13,2/112,5. 10—12. *Tricolporopollenites miniverrucatus* Roche 1968, prep.: PB-3-1, cross-table number: 18,9/113,5. ×1000

Germinal exine. — Tectum attenuating near pores in direction of pollen centre (3 and 7, Plate II). Columellar layer largely unchanged, foot layer slightly thickening anteriorly to pores, forming annulus and gradually tapering coalescent with tectum (3 and 7, Plate II). Endexine much more definite in pore region than extragerminally; this layer constituting also pore membrane.

As against the original description by the optical microscope (KEDVES 1965), a substantial deviation appears in the stratification of the exine. The layer denoted endexine formerly is identical with the foot layer, while the intragranulate structure indicates the columellar layer. The surface described as chagrenat might have been caused by the reflexion of the tectal perforation, or of the columellar layer. The demonstration of the endexine with lamellar ultrastructure in the extragerminal region is not likely by optical microscopic means at least in this. On the other hand, the pore membrane is well demonstrable on many examined specimens.

Transdanubiaepollenites n. fgen.
Fgen. typus: *T. magnus* n. fsp.
(4—7 in Plate III; 1—5 in Plate IV)

Note. — The new form-genus is described from the Lower Eocene layers of Úrkút. Sixty specimens were examined with optical microscope. The data of ultrastructure were also used in the descriptions.

Optical microscopical diagnosis

Tricolpate pollen grains: pole axis always shorter than equatorial diameter. Sculpture reticulate, surface ornamented in reticular lumen.

TEM Diagnosis

Exine consisting of ectexine and endexine. Tectal elements and columellar layer forming a reticulate ornamentation. Foot layer thin in comparison with endexine, latter one with a fibrillar ultrastructure.

Derivatio nominis: From Transdanubia, the locality of the generotype.

Differential diagnosis: It is well distinguishable from the form genera *Retitricolpites* (VAN DER HAMMEN 1956) VAN DER HAMMEN and WIJMSTRA 1964, and *Reticulataepollis* W. Kr. 1959, by the markings in the reticular lumen.

Transdanubiaepollenites magnus n. fsp.
(4—7 in Plate III; 1—5 in Plate IV)
Optical microscopical diagnosis

Equatorial contour largely spheroid. Colpi widening towards contour (3—4 μ), their lenght 20—30μ. Columellar layer 3—4 μ high, reticula pentagonal or hexagonal, from above diameter of their lumen 3—8 μ, in general 5—6 μ. Surface in reticular lumen decorated with baculate or granulate elements.
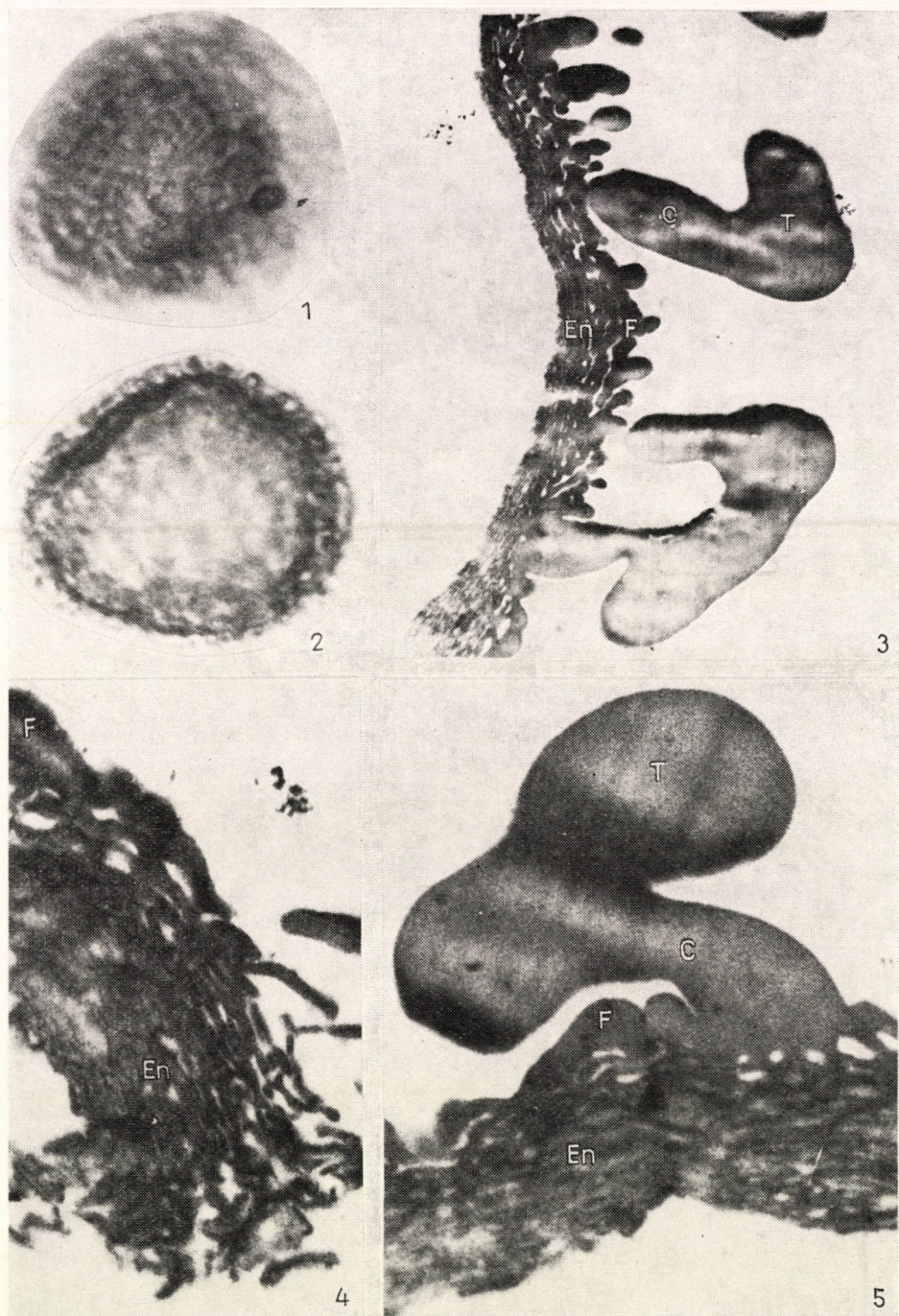
Plate IV. Transdanubiaepollenites magnus n. fgen. et fsp. 1, 2. Optical microscopical picture of embedded specimen, examined ultrastructurally, ×1000. 3. Section of extragerminal exine ultrastructure. ×10 000. 4. Endexine ultrastructure near germinal region. ×25 000. 5. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer, En = endexine

Maximum size: 38—55 μ
Holotype: prep. Ú-218—13/9 (4—7, Plate III); cross-table number: 19.2/117.5.
Locus typicus: Úrkút, Lower Eocene.
Stratum typicum: gray, miliolinal marl.
Derivatio nominis: Referring to its relatively large size.

Botanical relationship: Its optical microscopical morphology is similar to that of *Nyctaginaceae*, *Bougainvillea* and *Abronia* after the work of ERDTMAN (1952).

TEM Diagnosis

Exine consisting of ectexine and endexine. Tectum and columellar layer forming characteristic reticulate ornamentation. Foot layer thin, reticular lumen is ornamented with baculi or granulae. Endexine of fibrillar ultrastructure, its thickness extragerminally equaling that of tectum, while its elements slightly increasing towards germinals T/C/F = 4—5/7—10/1.

Concerning its ultrastructure, the extremely thin foot layer should be emphasized, hitherto not found in the species examined.

Tricolporopollenites sooi n. fsp.
(8 and 9; Plate III; 1—6 Plate V)

The sample material originates from the Lower Eocene layers of Úrkút (Borehole No. U-218). Hundred exemplars of the form-species underwent optical microscopical investigations.

Optical microscopical diagnosis

Tricolporate pollen grains, contour slightly ellipsoid or almost spheroid in equatorial view. Surface uneven, exine intrabaculate. A less structured zone of 1.5—3 μ width beside. Colpus narrow, not reaching poles. Endopore ellipsoid or rectangular, its average size 5.6 × 2.6 μ.
Maximum size: 20.5—31.5 μ.
Holotype: Prep. Ú-218—13/9, cross-table No.: 13.2/112.5; 8 and 9, Plate III.
Locus typicus: Úrkút, Lower Eocene.
Stratum typicum: Gray miliolinal clay marl.
Derivatio nominis: Dedicated to Professor REZSŐ SOÓ.

Differential diagnosis: The structure of the colpi and the pores well distinguish it from *Tricolporopollenites kruschi* (R. Pot. 1931) Th. and Pf. 1953, subfsp. *analepticus* (R. Pot. 1934) Th. and Pf. 1953.

Botanical relationship: on the basis of its optical microscopic morphology, the family *Pandaceae* is the most likely.

TEM Diagnosis

Exine dividing into ectexine and endexine; latter one of granulate ultrastructure Ectexine tectate, perforate. Tectum and columellar layer attenuating toward colpi. By a multiplication of its elements, endexine markedly thickening along colpus T/C/F = 1.5—2/1/3—4.

Optical microscopical results

Of the 100 specimens, 90 had fossilized in the polar view or compressed laterally, and only 10 equatorially. Maximum diameters from 20.5 μ to 31.5 μ; specimens with 23.5—26.5 μ and 30 μ occuring frequently. When viewed equatorially, contur slightly ellipsoid or almost circular; polar axis in general shorter than equatorial (22.5 × 23.5 μ). Length of colpi 9—14 μ, averaging 11 μ. Along colpi a less structured part, its width 1.5—3 μ near pores; in general 2.1 μ. Pores ellipsoid or approximatelly rectangular, their average size 5.6 × 2.6 μ. Tectate exine discernible also by optical microscopice.
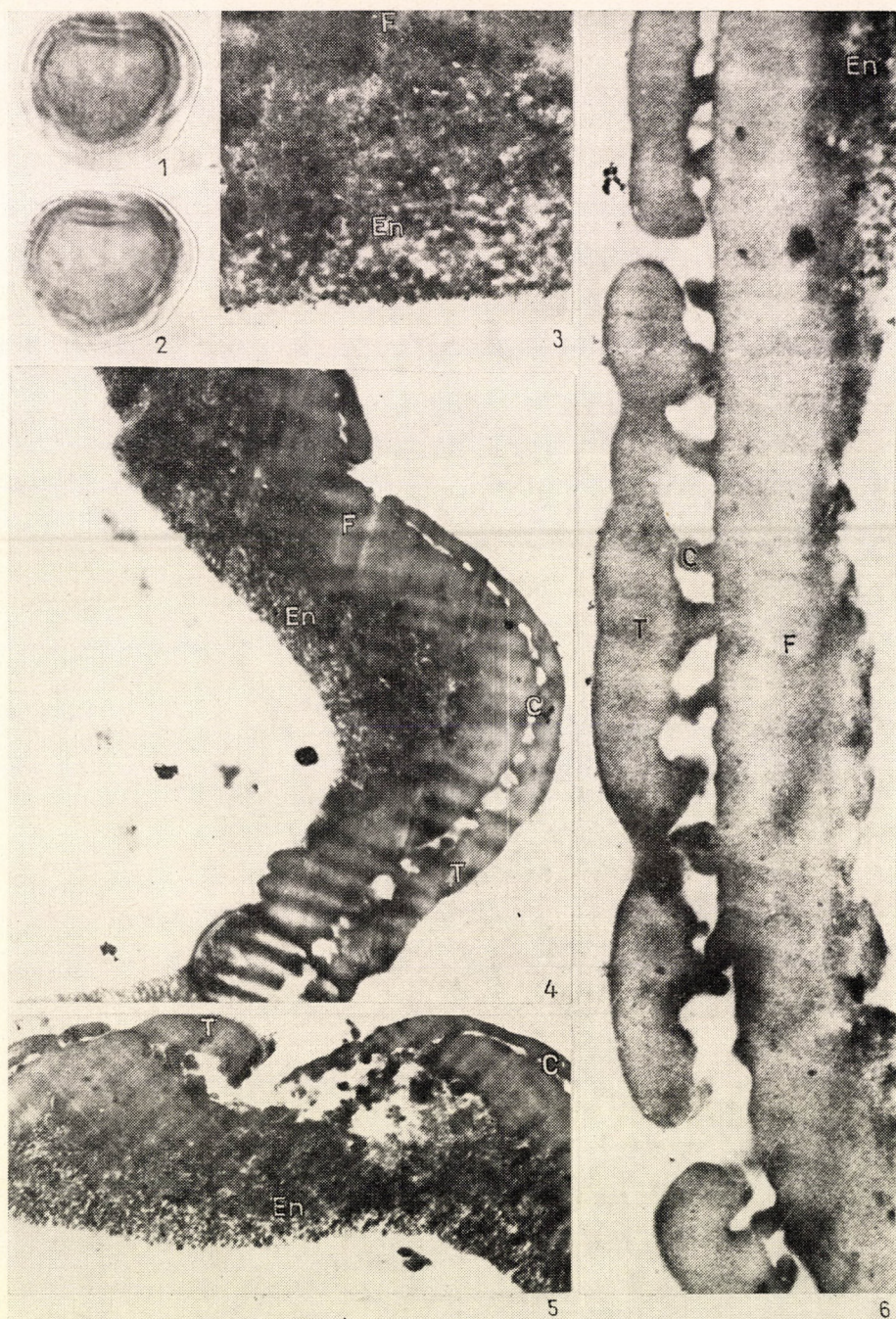
Plate V. Tricolporopollenites sooi n. fsp. 1, 2. Optical microscopical picture of embedded specimen, examined ultrastructurally. ×1000. 3. Foot layer and endexine with thickened granulate ultrastructure in germinal region. ×25 000. 4, 5. Ultrastructure of germinal region. ×10 000. 6. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer, En = endexine

Electronmicroscopical results

Extragerminal exine.—Tectate, perforate (6, Plate V), perforations occuring fairly seldom. Tectal surface uneven. Columellar layer well distinct, its elements straight or obliquely columnar. Foot layer much thicker than tectum. Under it endexine of indistinct thin granular ultrastructure.

Germinal exine.—Tectum and columellar layer attenuating towards germinal region (4 and 5, Plate V); ectexine interrupted in colpus (5, Plate V). Endexine strongly thickening by an increase of its elements in germinal region (3—5, Plate V), its granulate ultrastructure well observable.

Tricolporopollenites miniverrucatus Roche 1968 (10—12, Plate III; 1—6, Plate VI)

The examined material originates from the Sparnacian deposits of the Parisian Basin.

Extragerminal exine.—Tectate, perforated (3 and 6, Plate IV). Surface tectum uneven, diameter of perforations varying. Columellar layer deviating from exines of fossile *Dicotyledonopsides* examined so far, consisting of two kinds of elements: from the so-called regular, more or less radially arranged elements of columnar shape and from ultrastructure elements of minute spherical forms. Thickness of foot layer largely agreeing with that of tectum (T/C/F = 1/1.5/1—1.5) with an extremely thin layer (its electron affinity markedly deviating from the previous ones) probably the endexine, under it.

Germinal exine. — Since the ultra-thin sections were prepared in the direction of the longitudinal axis of the pollen and no complete series could be assembled, the ultrastructural results are not complete. One of the important elements of the germinals is the foot layer (4 and 5, Plate VI) in the middle of which there is a cleavage narrowing towards the poles, with the pore lying meridionally (5, Plate VI).

Tricolporopollenites krutchi (R. Pot. 1931) Th. and Pf. 1953 subfsp. *accessorius* (R. Pot. 1934) Th. and Pf. 1953 (1—6, Plate VII)

The examined material originates from the Sparnacian deposits of the Parisian Basin.

Extragerminal exine. — Tectate, perforate; perforations fairly narrow, surface of tectum uneven, with smaller or greater constrictions (3 and 6, Plate VII). Columellar layer relatively thin, consisting general of columnar radial elements. Foot layer somewhat thinner than tectum T/C/F = 3/1/2. Endexine not distinct in extragerminal region.

Germinal exine. — Ultrastructurelly granulate endexine a considerable constituent of colpus; pore observed on this layer (4 and 5, Plate VII).

Unfortunately, there are no satisfactory data on the germinal ectexine.

Tricolporopollenites cingulum (R. Pot. 1934) Th. and Pf. 1953 subfsp. *pusillus* (R. Pot. 1934) Th. and Pf. 1953 (1—8 in Plate VIII)

The examined material derives from the Lower Eocene layers of Úrkút (Borehole No. U-209). A very frequent and significant pollen in deposits from the Tertiary; from taxonomical and nomenclatorial aspects, the "cingulum group" is rather problematic. Two specimens were examined, giving in essence identical results.
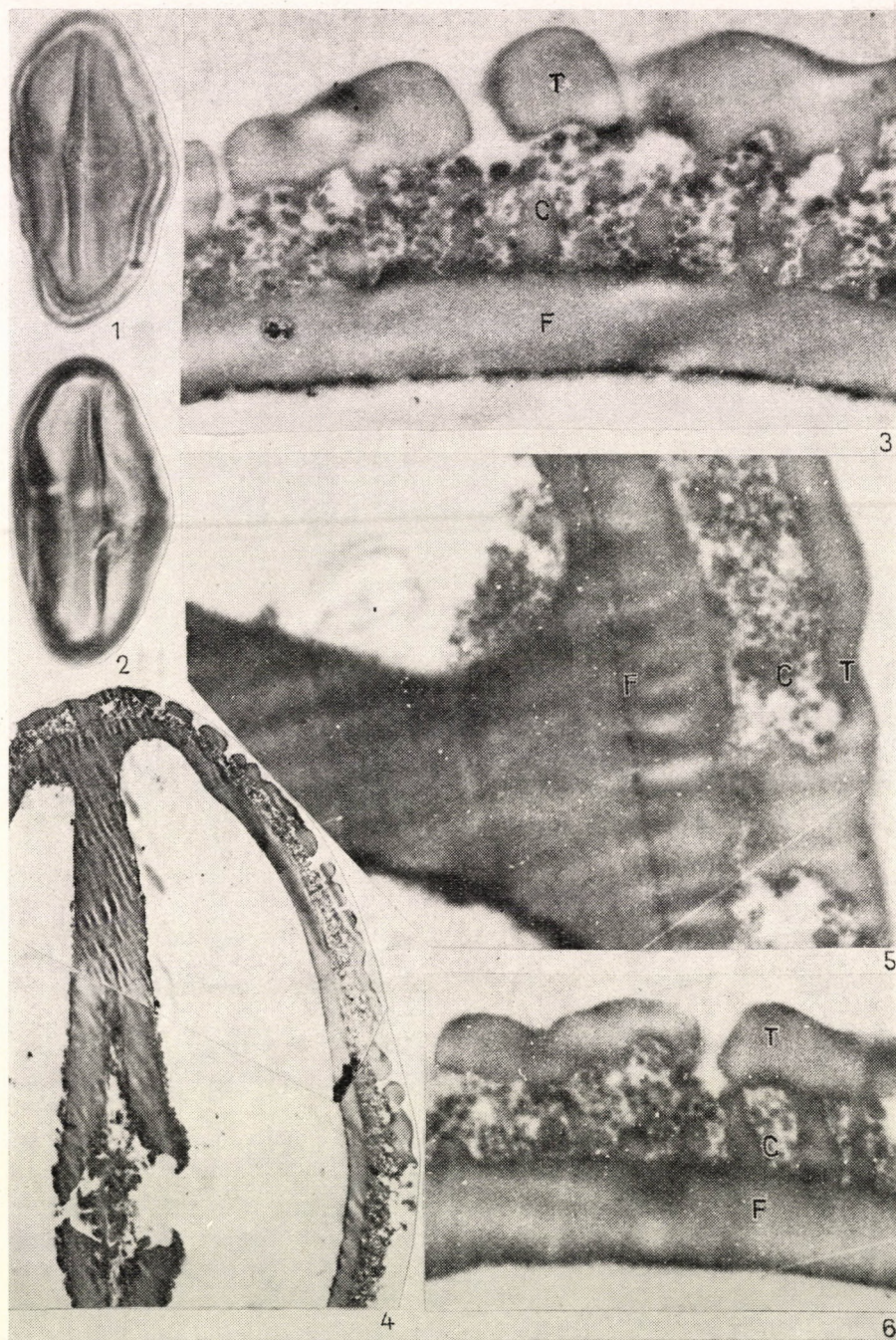
Plate VI. Tricolporopollenites miniverrucatus Roche 1968. 1, 2. Optical microscopical picture of embedded specimen, examined ultrastructurally. ×1000. 3. Section of extragerminal exine ultrastructure. ×25 000. 4. Ultrastructure of pollen grain apex at level of germinal foot layer. ×25 000. 5. Survey of exine ultrastructure of the pollen grain examined. ×5000 6. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer

Plate VII. Tricolporopollenites kruschi (R. Pot. 1931) Th. et Pf. 1953 subfsp. *aceessorius* (R. Pot. 1934) Th. et Pf. 1953. 1, 2. Optical microscopical picture of embedded specimen, examined ultrastructurally. ×1000. 3. Section of extragerminal exine ultrastructure. ×25 000. 4, 5. Survey of germinal region ultrastructure. ×5000. 6. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer, En = endexine
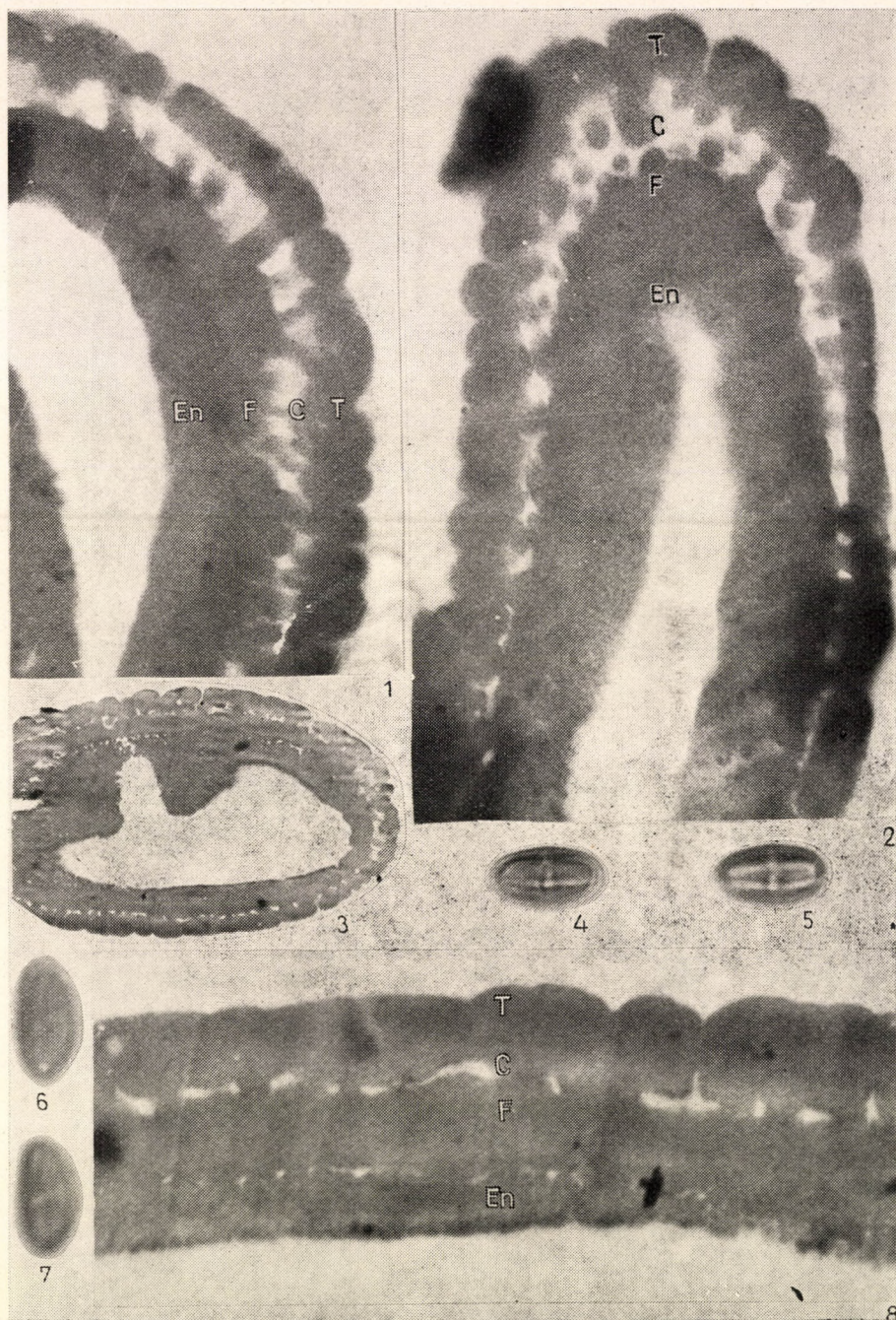
Plate VIII. Tricolporopollenites cingulum (R. Pot. 1934) Th. et Pf. 1953 subfsp. *pusilus* (R. Pot. 1934) Th. et Pf. 1953. 1, 2. Ultrastructure of extragerminal region at apex of pollen grain. ×25 000. 3. Survey of pollen grain ultrastructure. ×5000. 4, 5. Optical microscopical picture of examined specimen, in embedding medium. ×1000. 6, 7. Optical microscopical picture of examined specimen in embedding medium. ×1000. 8. Section of extragerminal exine ultrastructure. ×25 000. T = tectum, C = columellae, F = foot layer, En = endexine

Extragerminal exine: — Tectate, surface of tectum uneven, with constrictions and locally transversed by channels (1, 2 and 8, Plate VIII). Columellar layer relatively thin, its elements in general short, columnar. Foot layer largely as thick as tectum. Endexine fairly in extragerminal region, with a granular ultrastructure.

Germinal exine. — Ultrathin sections showing meridionally situated pore on endexine. Granulate ultrastructure of endexine more distinct in this part than extragerminally (3, Plate VIII).

Tricolporopollenites cf. *microreticulatus* Pf. and Th. 1953 (1—3 in Plate IX)

The examined material originates from the Sparnacian layers of the Parisian Basin. The prepared pollen grains derive from a pollen cluster which, assumably fossilized when they were not yet completely mature. For the time being, only the extragerminal exine is known, consisting of ectexine and endexine. Ectexine tectate, perforated, perforations locally large hence tectum resembling capitula of "iliacoid pollen grains" (3 Plate IX). Reticulate structure of tectum well recognizable in tangential sections. Tectum projecting above columellar layer, its elements columnar; foot-layer relatively thin, T/C/F=2/6—3/1. Endexine somewhat thicker than foot-layer deviating from it by its electron affinity.

The ultrastructure of these pollen grains may to a certain extent be related to that of *Tricolporopollenites margaritatus* (R. Pot. 1931) Th. and Pf. 1953 f. *medius* Pf. and Th. 1953 examined previously (KEDVES and PÁRDUTZ 1970b).

Polycolpites viesenesis W. Kr. 1961 (4—6, Plate IX)

The examined material originates from the Lower Eocene layers of Úrkút (Borehole No. U-209).

For the time being, data are available only on the extragerminal exine of this pollen grain, important from the point of view of the Paleocene — Lower Eocene spore-pollen assemblages. Ectexine tectate, inperforate, surface of tectum even. Columellar layer extremely thin, its elements short, columnar (5, Plate IX). Foot layer 2—2.5 times thicker than tectum. No endexine could be demonstrated with certainty.

Discussion of results

Summarizing the present results and those reported in the previous study, we have data on the ultrastructure of the following *Angiospermatophyte* pollen grains from the Lower Eocene:

BREVAXONES

Normapolles

Basopollis basalis (Pf. 1953a) Pf. 1953b
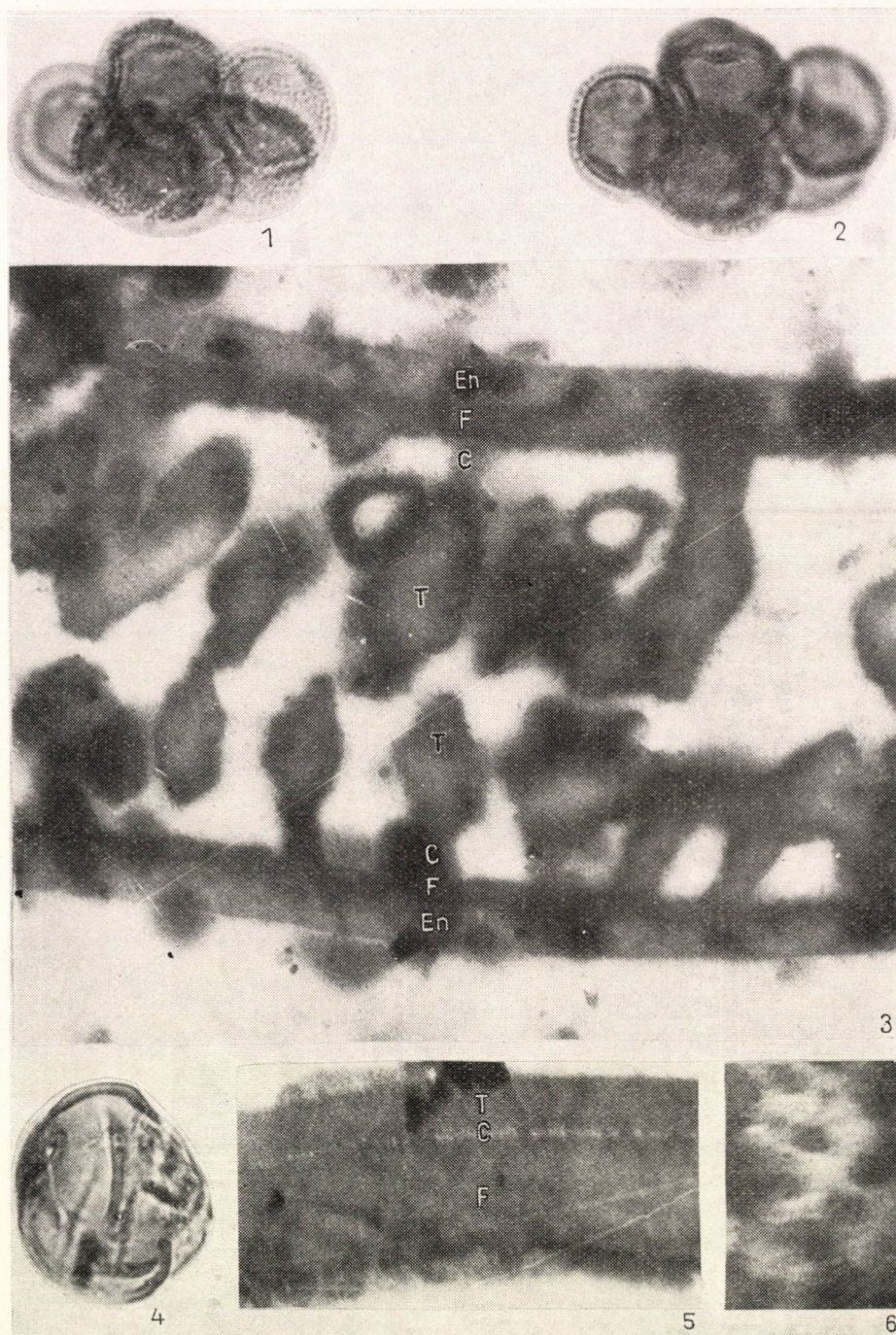
Plate IX. Tricolporopollenites cf. *microreticulatus* Pf. et Th. 1953. 1, 2. Optical microscopical picture of examined pollen cluster in embedding medium. ×1000. 3. Section of exine ultrastructure extragerminal at the contact between two pollen grains. ×25 000. *Polycolpites viesenensis* W. Kr. 1961. 4. Optical microscopical picture of embedded specimen, examined ultrastructurally. ×1000. 5. Section of extragerminal exine ultrastructure. ×25 000. 6. Tangential section of columellar layer. ×50 000. T=Tectum, C=columellae, F=foot layer, En=endexine

Pompeckjoidaepollenites subhercynicus (Pf. 1953b) W. Kr. 1967
Nudopollis terminalis (Pf. and Th. 1953) Pf. 1953b *hastaformis* Pf. and Th. 1953
Plicapollis pseudoexcelsus (W. Kr. 1958a) W. Kr. 1961d *turgidus* Pf. 1953a
Interpollis velum W. Kr. 1961d

Postnormapolles

Triporopollenites robustus Pf. 1953a
Subtriporopollenites constans Pf. 1953a *magnus* W. Kr. 1961d
Intratriporopollenites microreticulatus Mai 1961
Compositoipollenites rhizophorus (R. Pot. 1934b) R. Pot. 1960 *burghasungensis* Mürr. and Pf. 1953
Diporites iszkaszentgyörgyi Kds. 1965

Longaxones

Transdanubiaepollenites magnus n. fgen. and fsp.
Tricolporopollenites sooi n. fsp.
Tricolporopollenites miniverrucatus Roche 1968
Tricolporopollenites kruschi (R. Pot. 1931) Th. and Pf. 1953 *accessorius* (R. Pot. 1934) Th. and Pf. 1953
Tricolporopollenites cingulum pusillus (R. Pot. 1934) Th. and Pf. 1953
Tricolporopollenites margaritatus (R. Pot. 1931a) Th. and Pf. 1953 *medius* Pf. and Th. 1953
Tricolporopollenites cf. *microreticulatus* Pf. and Th. 1953
Polycolpites viesenensis W. Kr. 1961

The results relate to two groups of questions, viz. (1) the general morphological problem of fossile pollen grains, (2) the problem of describing morphological taxa.

1.1. No endexine could be demonstrated in Basopollis basalis, similarly to the case of the previous Eocene *Normapolles* exine. So the ultrastructure of this pollen grain of complicated construction also confirms the previous statement according to which the number of exine layers decreases in Eocene *Normapolles* taxa against the Upper Cretaceous ones, which is an evolutionary characteristic within the group. Since the endexine did not occur in the so-called "ancient type" *Postnormapolles* pollen grains (for example, in *Triporopollenites robustus*, *Subtriporopollenites constans magnus*) whereas it can be demonstrated with certainty in the *Compositoipollenites rhizophorus burghasungensis*, considered the "modern angiosperm" type, it can be inferred that the endexine may appear in the pollen grains of *Brevaxones* at different growth levels. The varying number of exine layers is of taxonomic value; this, however is not identical within the various types.

The annulus in *Basopollis basalis* comes into existence by the multiplication of the elements of the columellar layer, while the praevestibulum is an invagination of the germinal columellar layer along the pore channel. The vestibulum evolves by the foot layer separating in the pore region from the columellar layer. By this, and with previous results of similar character a considerable part of te most important fundamental conceptions relating to the germinal exine of fossile *Brevaxones* pollen grains could be clarified also on an ultrastructural basis.

1.2. The present study discussed the ultrastructure especially of *Longaxones*, and within it that of tricolporate pollen grains. This problem following also from its very nature is more complicated than that of the *Brevaxones* pollen grains. A fundamental disadvantage is that the ultrathin section are longitudinal sections, since the recognition of many form-species in the embedded material is very difficult, or impossible, in a polar position. Hence the ultrastructural of the germinal exine can be wholly clarified only by further examinations of a great number, and mainly by successful series, of sections.

On the basis of investigations made so far, the majority of the exines of pollen grains in the *Longaxones* examined consist of ectexine and endexine. The ectexine is tectate and — with the exception of *Polycolpites viesenensis* — perforate. A new type of the columellar layer was demonstrated in *Tricolporopollenites miniverrucatus*, where this layer consists of two kinds of ultrastructural elements. This has not been found in fossile ectexines so far, and no data of this nature was published in the literature dealing with the exine ultrastructure of the available recent pollen grains.

Three types of endexine were found to occur: fibrillar (e.g. *Transdanubiaepollenites magnus*), granular (e.g. *Tricolporopollenites sooi*), and the case when the endexine deviates from the foot layer only by its electron affinity (e.g. *Tricolporopollenites* cf. *microreticulatus*). The endexine is especially developed in the germinal region. As for the colpore, ROLAND's results (1968), obtained in recent pollen grains, are considerable and rendered a suitable basis for the evaluation of our fossile data. He established that the endoaperture (endopore) is on the innermost layer, the endexine, or in the absence of this on the foot layer. The endopore lying on the endexine could be demonstrated in *Tricolporopollenites kruschi* accessorius and *Tricolporopollenites cingulum* oviformis, where as in *Tricolporopollenites miniverrucatus*, where no endexine could be found with certainty, the endopore is on the foot layer. This ultrastructural characteristic may be considered a substantial feature when classifying fossile tricolporate pollen grains. From an ultrastructural evolutionary viewpoint the presence of endexine in tricolporate pollen grains should be assessed quite differently from the *Brevaxones* types, especially in *Normapolles* taxa, because endexine may be present as well as absent within the types of identical development, and there may be deviations even in their

ultrastructure. The problem will be furthered by the knowledge of the ultrastructure of the first definitely angiospermatous tricolpate and tricolporate pollen grains from the Upper Cretaceous but especially from the Lower Cretaceous.

2. As for the nomenclatorial and taxonomic problems, the followings should be considered: Without treating in detail the nomenclatorial literature of fossile sporomorphs (requiring a separate study today), one should point out the difficulties arising in the various fields owing to the numerous differing nomenclatures. Various studies discussed the intolerable situation, and attempts have been made for a uniform nomenclature at least within the individual geological ages but no considerable improvement has been achieved indeed, the situation is steadily becoming worse with the spread on a large scale of palynological investigations and the resultant creation of newer "schools". The number of form-genera and form-species described year by year is constantly increasing. HUGHES and STUART (1967) had several suggestions for moderation in the description of the new species. The application of new methods complicates to a certain extent the problems of taxonomy. As regards the importance of ultrastructural investigations of fossile exines, it is believed that there are sufficient data available to justify their necessity. The utilization of the scanning electronmicroscope on fossile pollen grains (e.g. REYRE 1968, REYRE, KIESER and PUJOL 1970) also sheds some fresh light on the earlier optical microscopical results. LEFFINGWELL, LARSON and VALENCIA (1970) have already carried out complex investigations (TEM, SEM and optical microscope) on a form-species (*Wodehouseia spinata* STANLEY 1961). A considerable part of the original optical microscopical diagnoses need indispensable complementation by the use of the electronmicroscopical method. On the other hand, the data on the ultrastructure have naturally also been utilized, in the description of new taxa given in the present study. (For the time being, it is considered reasonable to separate in the diagnoses the optical microscopical characteristics from the electronmicroscopical ones). Obviously, these diagnoses are of no identical value with those produced exclusively on the basis of optical microscopical investigations, but more perfect. Even more exact are the descriptions supported also by data obtained by the scanning electron microscope. There exists already a group of fossile, sporomorphs whose diagnostic data were obtained by modern methods of investigation against those aquired exclusively by the classical optical microscopical method. And further problems arise owing to differences in the level of knowledge relating to the individual sporomorphs. It is evident that numerous new taxa will be described still exclusively by the optical microscopical method; at present the requirement that a new taxon be described only by applying the triple method (optical microscopice, TEM and SEM) is wholly unreal, but it is desirable that results of a general character achieved so far

with the electronmicroscopical method should be considered in the descriptions. For example, it is not advisable to use the term endexine in optical microscopical descriptions, since it can be mixed up with the foot layer. If three layers can successfully be separated on the exine then they certainly are the three layers of the ectexine, viz. the tectum, the columellar layer and the foot layer. Another inference relates to attitude. It frequently occurs that certain authors "see" more layers in the course of optical microscopical investigations than exist; they describe a complicated lamellar system on the basis of reflexions. These will certainly be revised by the ultrastructural examination, but it is advisable to avoid this, and not to complicate by subjective considerations the often really complicated germinal exine structure.

As investigations will be continued and it is hoped that they will bring new results in the knowledge of fossile sporomorphs.

Summary

New results obtained by the ultrastructural investigation of Lower Eocene angiosperm pollen grains are submitted. Nine form-species were examined yielding one new form-genus (*Transdanubiaepollenites*) and one new form-species (*Tricolporopollenites sooi*). In describing the new taxa also electronmicroscopical data were utilized. The diagnosis of *Basopollis basalis* and *Diporites iszkaszentgyörgyi* were completed by ultrastructural data. The germinal exine of *Basopollis basalis* clarified the fine structure of the praevestibulum and the vestibulum. A new type of the columellar layer of the ectexine was established in *Tricolporopollenites miniverrucatus*. The endexine is rather frequent in fossile *Longaxones* pollen grains; three types are distinguished (lamellar, granulate, and one deviating from the foot layer only by its electron affinity). Similarly to the situation in recent pollen grains, the endoaperture of the tricolporate pollen grains appears in the endexine the innermost layer of the exine (Roland 1968), or in the absence of that on the foot layer.

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RELATIONSHIP BETWEEN STRUCTURAL AND FUNCTIONAL CHARACTERISTICS IN STEPPE-MEADOWS IN HUNGARY

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Correlations between weight dominance, diversity (structural characteristics) and productivity, energy flow, efficiency, turnover time (functional characteristics) have been studied on the basis of three year's phytobiomass measurements in two steppe plant communities (*Artemisio-Festucetum pseudovinae* and *Peucedano-Galatelletum punctati*). An inverse relationship has been established between weight dominance and diversity. Weight dominance and functional properties are inversely related, with the exception of turnover time. Functional characteristics are directly related among themselves, with the exception of turnover time, in an inverse relationship with the rest of the functional properties. The results partly run counter to certain observations reported so far.

The examination of relationships between structure and function is gradually coming into the fore in ecosystem research. This follows also from the fact that an ecosystem is considered a functional unity.

Since Lindeman's classical work (1942), the ecosystem has been divided into trophic levels. Considering the ecosystem as a whole, the trophic levels constitute its structure. Margalef (1963) writes about the structure of the ecosystem and says that it has structure in a sense that it is composed of various parts (producer organisms, consumer organisms, decomposer organisms), and that these parts are arranged according to a definite, distinct pattern. This definition may be completed by the addition that the state of being arranged guarantees the circulation of matter and the flow of energy.

Relationships between structure and function has been summarized by Odum (1962). Under structure he means (1) composition of biological community, number of species, their biomass, life cycle, and distribution; (2) quantity and distribution of abiotic materials; (3) range and gradients of conditions of existence. Under function belong in his work: (1) rate of biological energy flow, productivity, rate of respiration; (2) biogeochemical cycles; (3) biological and ecological regulation. To the above classification Odum adds that it can be suggested only in the interest of facilitating study. In a later paper Odum (1969) enumerates 24 ecosystem characteristics of which he regards only six as structural ones (organic matter, inorganic nutrients, species diversity — variety component, species diversity — equatability component, biochemical diversity, stratification and pattern diversity).

Structure and function can also be distinguished within the various trophic levels. No investigations have been carried out concerning the influence of structure and function within the various trophic levels (subsystems) on the system as a whole, probably because of the difficulties of investigation and analysis.

Dealing with the relationship between structure and function of the producer organisms of the ecosystem (producer subsystem), ODUM (1960) regards species composition and species diversity as structural characteristics, while productivity as a functional one. GOLLEY (1965) examined ten structural characteristics, ranging from physiognomy to chlorophyll quantity. Among the functional characteristics he examined productivity, rate of respiration and decomposition of litter, and energy budget. MCNAUGHTON (1967, 1968) writes only about functional characteristics, among which he discussed dominance and species number.

In this study the relationship between some structural (weight percentage dominance and diversity) and functional (productivity, energy flow rate, efficiency, turnover time) characteristics of the producer subsystem are discussed.

Area of investigation

The investigation was carried out in the IBP sample area at Újszentmargita, in two plant communities considered ecosystems. *Artemisio-Festucetum pseudovinae* (= *Artemisietum*) and *Peucedano-Galatelletum punctati* (= *Peucedanetum*). The characterization and elaboration of the communities are given in the studies by MÁTHÉ—PRÉCSÉNYI—ZÓLYOMI (1967), MÁTHÉ—TALLÓS (1967), MÁTHÉ—TALLÓS—ZÓLYOMI (1967), PRÉCSÉNYI (1969), ZÓLYOMI—PRÉCSÉNYI (1970).

Material and method

Harvest samples were taken three times (in April, June and September) in the growth periods between 1967—1969. The harvested material was selected into main components and weighed after drying at 105°C.

The index of diversity (ID) was calculated by means of the SHANNON formula ($-\Sigma p_i \log_2 p_i$, where p_i was estimated from the weight percentage), on the basis of the weight percentage of the living aboveground parts (WILHM 1968, PRÉCSÉNYI 1969).

By productivity, energy flow, efficiency and turnover time the formulas are meant as follows:

productivity:

$$d\ \mathrm{cal}_f \cdot s^{-1} \cdot (dt)^{-1};$$

energy flow:

$$\frac{d\ \mathrm{cal}_f \cdot s^{-1} \cdot (dt)^{-1}}{\mathrm{cal}_b \cdot s^{-1}};$$

efficiency %:

$$100 \times \frac{d\ \mathrm{cal}_f \cdot s^{-1} \cdot (dt)^{-1}}{d\ \mathrm{cal}_r \cdot s^{-1} \cdot (dt)^{-1}};$$

furnover time:

$$\frac{cal \cdot {}_{max\text{-}f} \cdot s^{-1}}{d\ cal_f \cdot s^{-1} \cdot (dt)^{-1}};$$

where the symbols: cal_r = by solar radiation incoming caloric quantity; cal_b = caloric content of biomass; cal_f = caloric content of vegetation (phytobiomass); $cal_{max \cdot f}$ = maximum caloric content of vegetation; s = area unit; t = time unit.

For estimating the energy flow, the caloric content of the phytomass was taken at t_1 time, after ODUM (1960). Caloric designation has been used in the analysis because this considered appropriate; the basic importance of productivity is fairly evident, and it appears in all further characteristics.

Conclusions are drawn from the triannual investigation of the two plant communities, on the basis of the three months' average of the measurements (underground plant parts have not been considered).

Table 1

Weight percentage of dominant species and ID values in Artemisietum and in Peucedanetum

Artemisietum					
Year	*Festuca pseudovina*	*Artemisia maritima*	Other species	Total %	ID
1967	58	29	13	100	1.36
1968	61	31	8	100	1.24
1969	55	31	14	100	1.39

Peucedanetum					
Year	*Peucedanum officinale*	*Gramineae*	Other species	Total %	ID
1967	30	53	17	100	1.44
1968	28	50	22	100	1.49
1969	31	50	19	100	1.48

Table 2

Productivity, energy flow, efficiency and turnover time of Artemisietum and Peucedanetum

Plant community	Year	Productivity	Energy flow	Efficiency	Turnover time
Artemisietum	1967	1.10	0.28	0.17	1.58
	1968	0.75	0.24	0.14	1.92
	1969	1.53	0.34	0.30	1.70
Peucedanetum	1967	2.12	0.53	0.36	1.15
	1968	0.43	0.12	0.08	1.78
	1969	1.94	0.59	0.41	1.08

In the *Artemisietum, Festuca pseudovina* is weight dominant, with *Artemisia maritima* in the second place. In the *Peucedanetum*, grasses (mainly *Alopecurus pratensis*) are dominant when treated together; *Peucedanum officinale* is not dominant, and this is why the groups were arranged in this way (Table 1).

Table 2 shows the productivity of the communities, their energy flow, efficiency and turnover time.

Results and discussion

The correlation coefficients between the various characteristics are shown in Table 3; measurement values are shown in Fig. 1 (productivity, efficiency etc. data in the cases of dominance percentage and ID for 1968 in the *Peucedanetum* have been omitted from the calculations and from the figures, as in our opinion to include them would have been misleading).
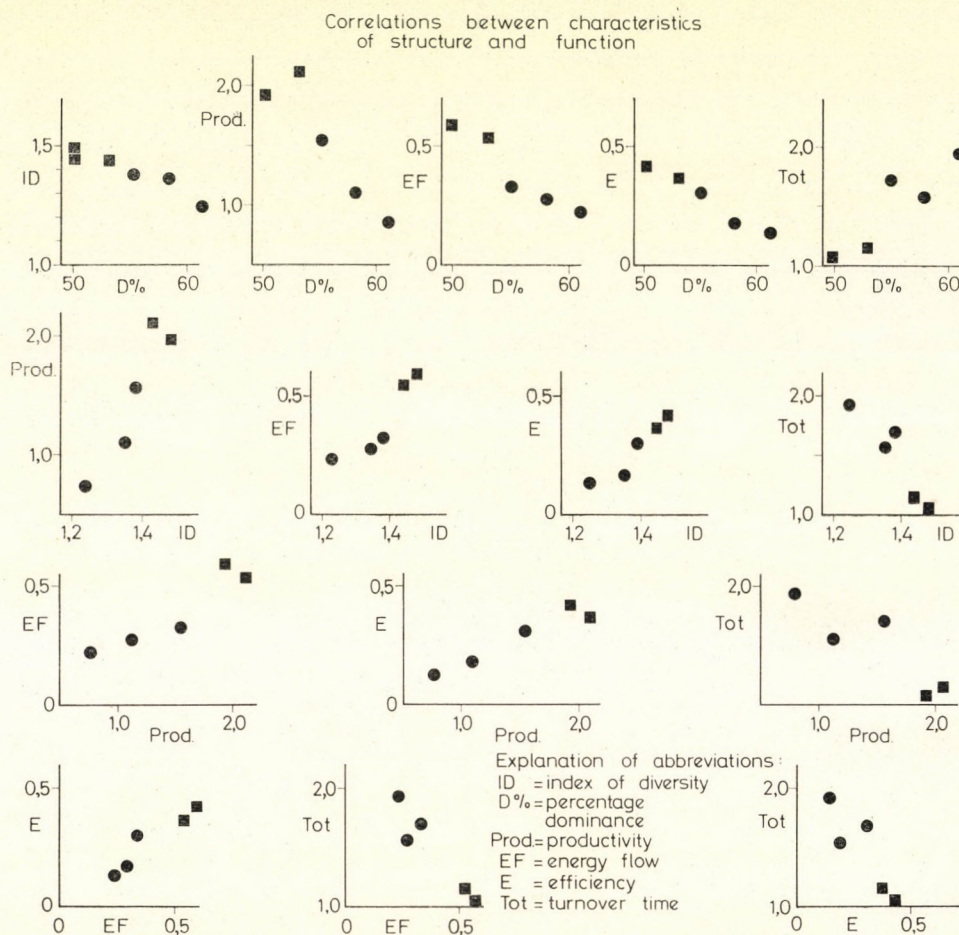
Fig. 1. Relationships between structural and functional characteristics. ● *Artemisietum,* ■ *Peucedanetum*

There is a negative correlation between the dominance percentage and the ID, as already pointed out by MARGALEF (1963), WHITTAKER (1965), MCNAUGHTON (1967, 1968), SINGH and MISRA (1969) and PRÉCSÉNYI (1969). This negative correlation theoretically follows from the definition of diversity. The more dominant a species becomes the smaller the diversity index is and vice versa. In our studies we arranged groups of three so that we could calculate the ID value from the same number of members. A maximum value of ID appears if each grup shows a 33 per cent share; the value of ID is 1.58 bit in this case.
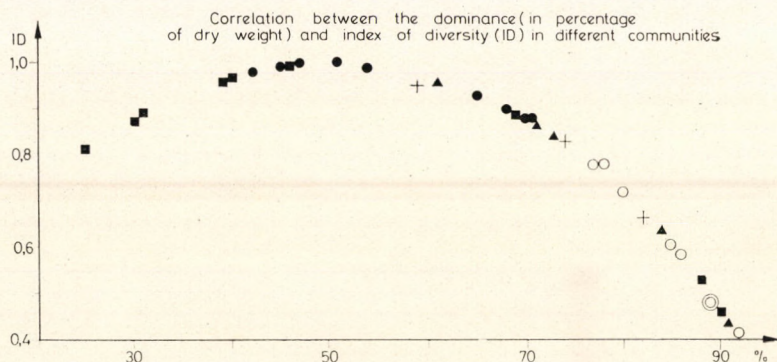
Fig. 2. Relationship between dominance and diversity. ● *Artemisietum* (April, June, September, 1967—1969). ■ *Peucedanetum* (April, June, September, 1967—1969). ○ *Achilleo-Festucetum* (grazed area, 1967), + *Achilleo-Festucetum* (grazed area, 1968), ▲ *Achilleo-Festucetum* (ungrazed area, 1968)

On the basis of their investigations in (1967—1968) MÁTHÉ and PRÉCSÉNYI (1970) published phytobiomass weight values from the same sample area for grazed and ungrazed *Achilleo-Festucetum pseudovinae*. On the strength of their study it can be stated that *Festuca pseudovina* is the weight dominant species. By inference from groups of two (also the data of *Artemisietum* and *Peucedanetum* were here recalculated), a negative correlation appears between the percentage of weight dominance and the ID value (Fig. 2). As is to be seen from this Figure, the correlation is not linear and the curve reaches its maximum at a 50 per cent dominance, as follows from the calculation with groups of two.

As is clear from Table 3, there is a positive correlation between productivity, energy flow and efficiency, and these same have an inverse correlation with turnover time. A negative correlation exists between the dominance percentage and the ID; it follows that the characteristics showing a negative correlation with the dominance percentage present a positive correlation with the ID.

Table 3

Correlation coefficients between structural and functional characteristics

	Diversity	Productivity	Energy flow	Efficiency	Turnover time
Dominance	−0.976**	−0.934*	−0.950*	−0.980**	+0.905*
Diversity	—	+0.930*	+0.896*	+0.923*	−0.915*
Productivity		—	+0.959**	+0.968**	−0.871*
Energy flow			—	+0.968**	−0.920**
Efficiency				—	−0.854*

* significant at 5% level
** significant at 1% level

A negative correlation can be established between the dominance percentage and productivity and between energy flow and efficiency, but a positive one concerning turnover time (Table 3 and Fig. 1).

These statements do not agree with ODUM's (1960) and McNAUGHTON's (1967, 1968) observations, according to these authors there is a positive correlation between dominance percentage and productivity, in other words, the correlation between diversity and productivity is negative. On the other hand, GOLLEY (1965) writes about an inverse relationship between these same properties. According to SINGH and MISRA (1969), diversity raises efficiency, while dominance makes the system stable and thus less efficient. PATTEN (1963) drew the conclusion that the correlation between diversity and productivity is positive. Otherwise, the results obtained by GOLLEY, SINGH and MISRA, PATTEN, and the present author are contrary to these given by ODUM and McNAUGHTON. An inverse relationship between energy flow and diversity is mentioned in MARGALEF (1963) and PRÉCSÉNYI (1970). This correlation, as can be seen in Table 3, is positive. MARGALEF's remark (1968) that the increase in energy flow reduces the stability of the system is in agreement with our observation. LEIGH (1965, 1968) pointed out that the higher are energy flow (which can be considered also a turnover time) and productivity the less stable is the plant community; by stability he means the resistance against fluctuation. Since energy flow is closely related to turnover rate and time, also according to LEIGH's remark (1965), McNAUGHTON (1967, 1968) considers turnover time as estimation of stability; by a better definition it could be termed the estimation of resistance against environmental variability. The inverse relationship between turnover time and other functional characteristics, e.g. that between productivity and turnover time, has been pointed out also by McNAUGHTON (1967, 1968). In Fig. 3 the correlation between turnover time and productivity in the main vegetation types is shown, on the basis of PRÉCSÉNYI's study (1971). As can be seen in the Figure, forests occupy a place

separate from the non-forest vegetation types, and an inverse relationship appears in both cases.

If turnover time as an estimation of resistance against fluctuation is accepted, the coniferous forests, deserts and tundras appear as most resistant against environmental fluctuation, as was to be expected on the basis of OLSON's study (1963) who pointed out that the rate of decomposition is slow in coniferous forests but high in tropical forests. This can be explained by the fact that turnover time in coniferous forests is long, while in tropical forests short.
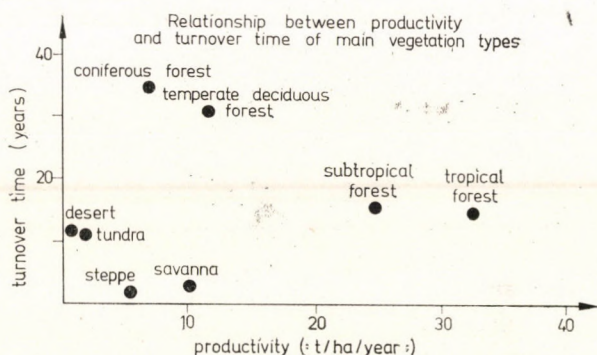
Fig. 3. Relationship between productivity and turnover time in the main vegetation types of the earth

On the basis of the foregoing discussion, McNAUGHTON's conclusions cannot be considered valid in general. One may concur with SINGH and MISRA's remark: "... much work has still to be done on all types of terrestrial systems before generalizations can be made for all situations".

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A HERBICIDE EFFECT IN THE MEIOSIS OF VICIA FABA

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The effect of the sodium salt of 2,4-dichlorophenoxy-acetic acid, Dikonirt, on the meiosis of *Vicia faba* was examined. With the increase of Dikonirt concentration, the number of dividing pollen mother cells decreased as compared with the values of control plants.

Introduction

Under the effect of pesticides and herbicides chromosome aberrations have been demonstrated in the breakdown of the root tip cells of barley, in the second generation after treatment (Wuu–Grant 1966a). Abnormal meiosis has been found also in the pollen mother cells (Wuu–Grant 1966b). On the examination of root meristem cells of *Vicia faba* chromosome aberrations caused by radiation were reported (Slotova–Karpfel 1960). In the root meristem cells of *Vicia faba* and *Pisum sativum* Dikonirt decreased the intensity of cell division and caused changes differing from the normal (Rojik–Horváth–Lontai 1969).

Material and method

Vicia faba plants were grown in glass-house and on open-air small plots in 6 replications until seed production. The following concentration series of Dikonirt was applied in tap-water solution on 1 m^2 surface: (the concentration of the substance in ppm) 2664, 1332, 666, 333, 166, 83, 28, 6, 3. Meiotic cell division was observed on the appearance of flower-bunds, in vitro at the age of 12–18 days, in vivo at the age 24–28 days. 20–40–60 flower-bunds of the treated and the control plants each were examined in every repetition. Photographs were taken of the fresh specimens coloured with carmin acidic acid.

Results and discussion

Dikonirt inhibited the growth of the plants, decelerated the reproduction period, and the flower-buds were distorted. In comparison with the control, the number of dividing pollen mother cells decreased with the increase in Dikonirt concentration. One series of our experiment is summarized in a table below.

Effect of Dikonirt in the meiosis of Vicia faba

	Number of cells		Cell division %
	examined	dividing	
Control	8396	1112	13.2
6 ppm	6700	732	10.92
166 ppm	12235	848	6.93
333 ppm	11480	146	1.2

Along with the decrease in the number of dividing cells, meiosis took place abnormally in the cells treated. Chromosomes adhered together, knotted, and chromatin bodies formed. An uneven distribution of chromatin substance could also be observed.

The lowest applied concentration of Dikonirt (6 ppm), — a rather high concentration for the plant from 2,4-dichlorophenoxi-acetic acid — inhibited but to a small extent the intensity of meiosis, as compared with the control (Photo 1, 2, 3, 4, 5).

As can be seen, a great number of abnormal changes, clods, bridges and distorted constructions formed. Owing to adherence, the course of meiotic division was inhibited. Elongation and knotting could be observed at 166 ppm treatment and the number of dividing pollen mother cells decreased (Photo 6, 7, 8). The smallest number of dividing pollen mother cells occured at 333 ppm
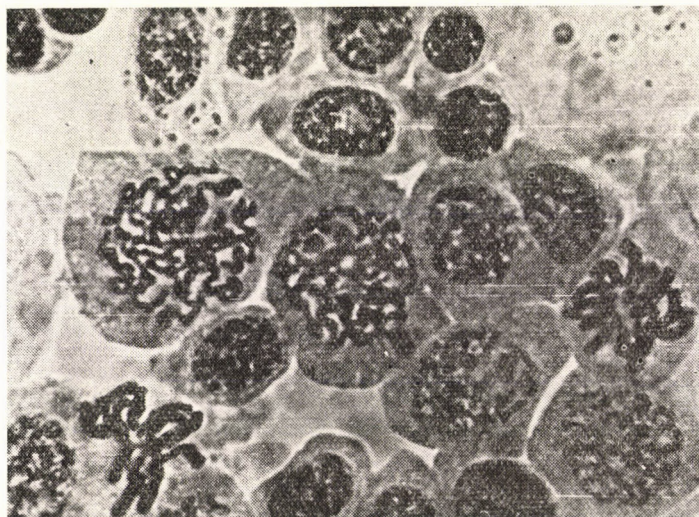
Fig. 1. Effect of 2,4-D on the meiosis of microspora mother cells of *Vicia faba.* 1, 2 (control, 800×); 3, 4, 5 (6 ppm, 980×); 6, 7, 8 (166 ppm, 800×); 9, 10, 11 (333 ppm, 800×)
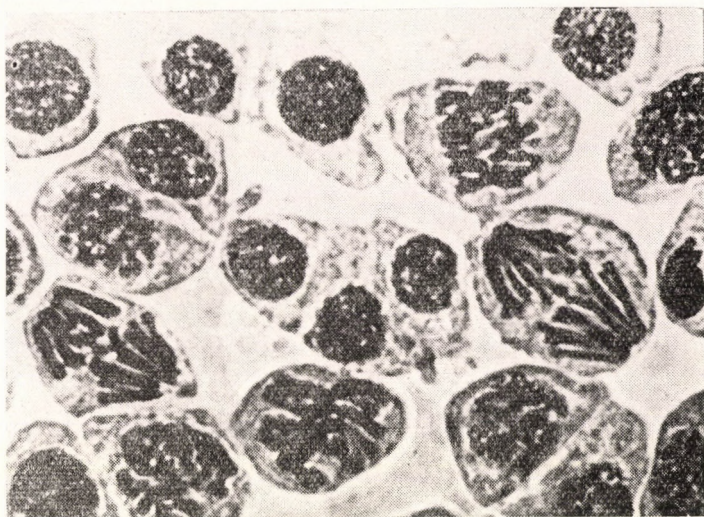
Fig. 2
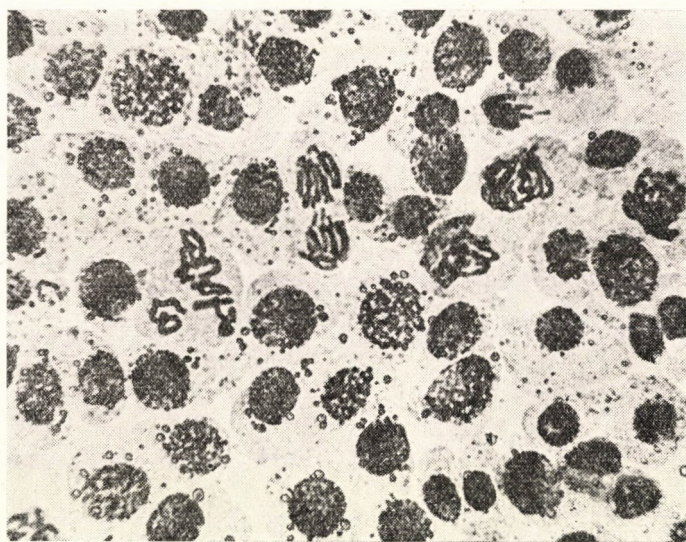
Fig. 3

treatment (Photo 9, 10, 11), where the coherence and amassing of chromatin can be observed.

Our observations are supported also by literature data: 2,4-D inhibits the growth of seedlings and also meiosis takes place in an abnormal way
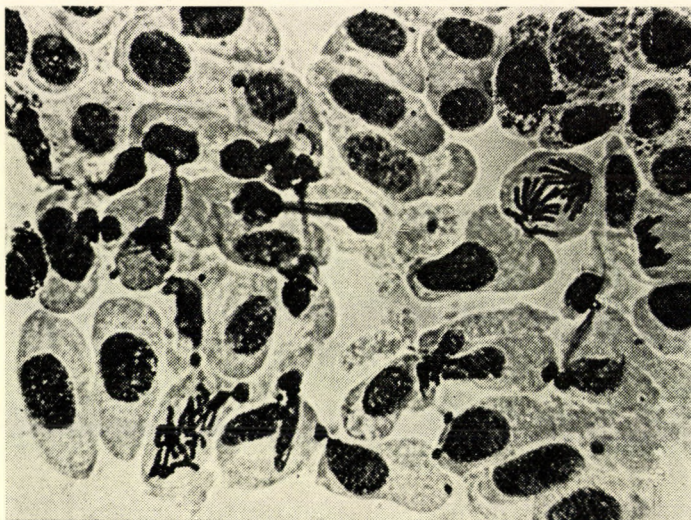
Fig. 4
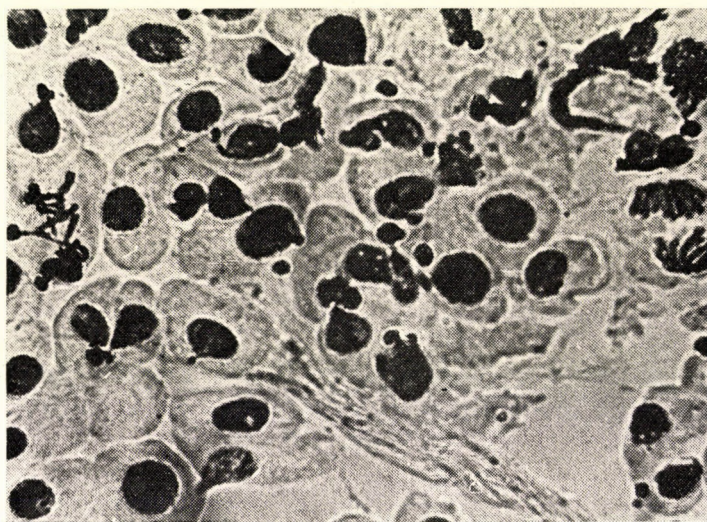
Fig. 5

(UNRAU 1952, 1953, 1954). 2,4-dichlorophenoxi-acetic acid stimulates the synthesis of RNA and of protein, enacted through the cell nuclei. It can associate with the free aspargin acid in the cells as peptid binds; the peptic bind forms gradually, and the protein synthesis depending on the DNA participates
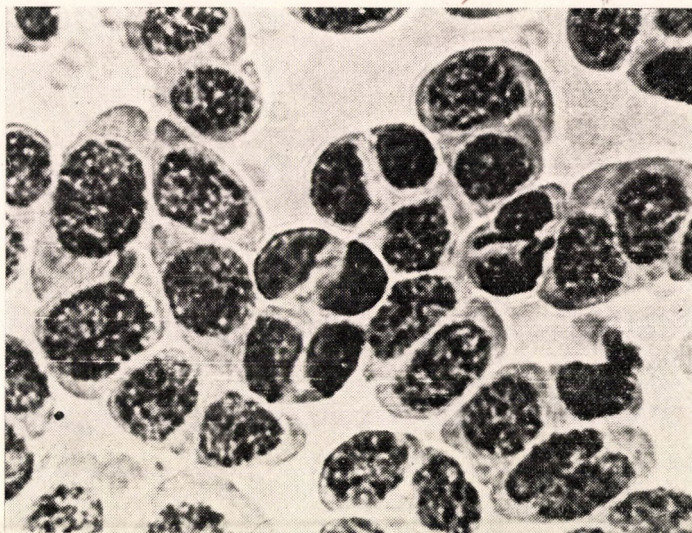
Fig. 6
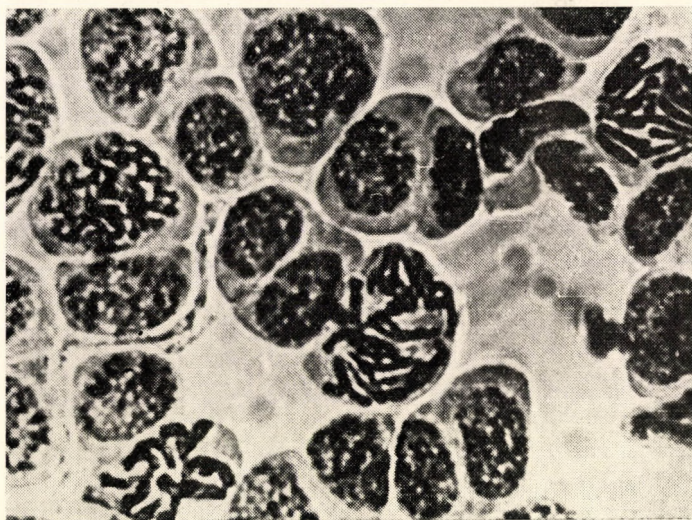
Fig. 7

in it. Applied in such high concentrations, 2,4-dichlorophenoxi-acetic acid disturbs the growth and the syntheses enacted through the cell nuclei, and assumably this is related also with the meiotic abnormalities.
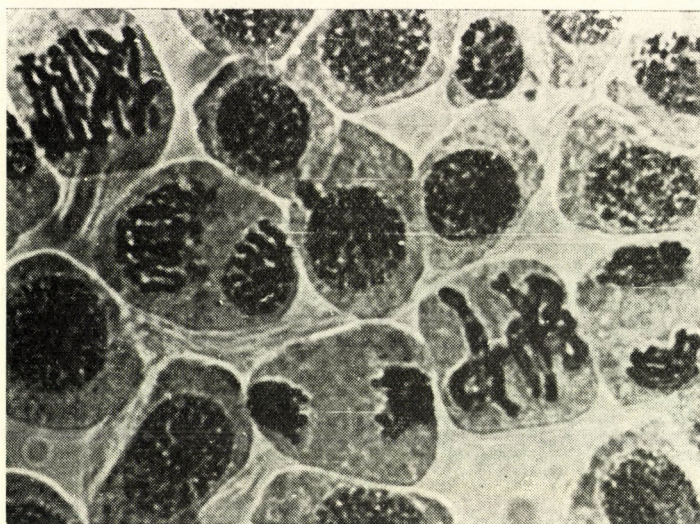
Fig. 8
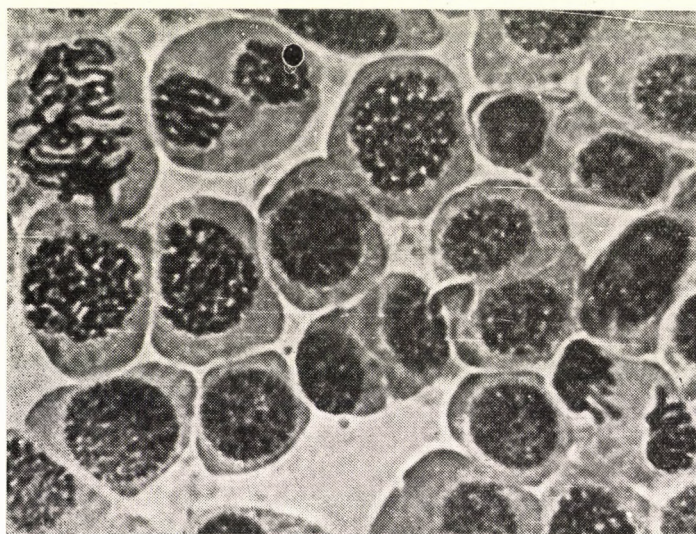
Fig. 9

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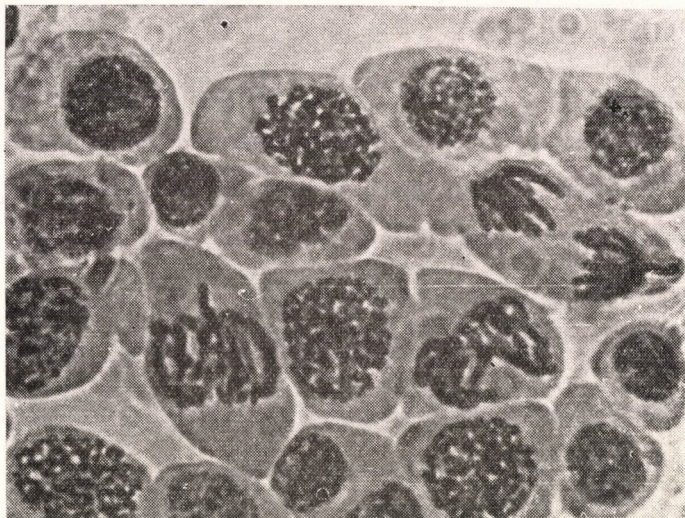
Fig. 10
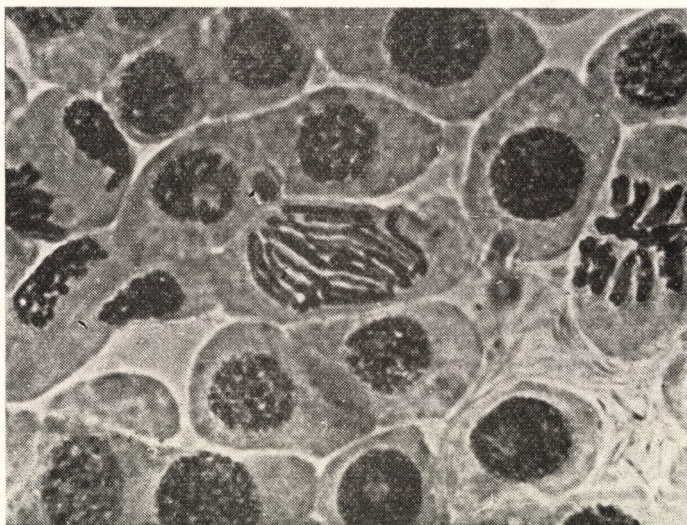
Fig. 11

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Acta Botanica Academiae Scientiarum Hungaricae, Tomus 18 (1—2), pp. 171—177 (1973)

NOMINA A NOBIS "NON RITE" PUBLICATA

Von

R. Soó

BOTANISCHER GARTEN DER L. EÖTVÖS UNIVERSITÄT, BUDAPEST

(Eingegangen am 13. Oktober 1971)

In my previous publications, especially in the series *Species et combinationes novae* 1—X (*Acta Bot. Hung.* **9** (1963) — **17** (1971), the name of the locality, collector and place of preservation of the type of numerous taxa was omitted, and sometimes (in certain studies in *Bot. Közl.*) also the basionym. Disregarding the comb. novae, of formal value only (and as such unimportant), here I make up for the data of the other taxa which were quoted incompletely, now these too are *nomina rite publicata.*

Nach den heute gültigen Regeln der internationalen botanischen Nomenklatur sind die neuen Taxonnamen seit 1. 1. 1958 nur dann rechtmässig [»gültig«] veröffentlicht, wenn der nomenklatorische Typus [möglichst Holotypus] angegeben ist. Es müssen auch die Namen des Fundorts, des Sammlers und des Herbars angegeben sein [Artikel 37]. Ebenso sind die Neukombinationen [comb. vel stat. nov.] seit 1. 1. 1953 (nach Artikel 33) nur dann gültig, wenn das Basionym [der ursprüngliche Name des Taxons] vollständig [nach Werk, Band, Seitenzahl, Jahreszahl] zitiert ist. Diese Umstände waren mir wohl seit vielen Jahren gut bekannt [besprach ich ja selbst die Nomenklaturregeln in ungarischer Sprache — Bot. Közl. **50,** 203—11, 1963], doch habe ich sie selbst nicht immer genau berücksichtigt. In der Aufzählung der Exsiccata des neuen Taxons wurde der Holotypus nicht immer hervorgehoben, bei unbedeutenden Formen oder Lusus nicht einmal erwähnt. Manche der letzteren wurden aufgrund der in der Literatur erwähnten, aber nicht benannten Abweichungen beschrieben (z. B. die *Convolvulus-arvensis*-Formen nach den Blütentypen von FEHÉR in Bot. Közl. **10,** 152—163, 1911], so dass kein Holotypus genannt werden konnte. Bei den Neukombinationen kam es öfters vor, dass die Jahres- oder die Seitenzahl zufällig ausblieb oder dass ich manchmal das genaue Zitat weder in Ungarn auffinden, noch eruieren konnte. In der Serie Regnum vegetabile wird seit 1966 in jedem Jahr ein Index to Europaean Taxonomic Literatur von R. K. BRUMMITT zusammengestellt und veröffentlicht [bisher 1965—69 erschienen]. Diese Indexe zählen alle im betreffenden Jahre publizierten neuen Taxa und neuen Kombinationen auf, wobei sie zwischen gültig und nicht richtig (»non rite«) publizierten Namen scharf unterscheiden. In diesen Indexen fand ich ziemlich viele der meinigen. Mr. BRUMMITT ist aber zu streng, denn zahlreiche der von ihm nicht anerkannten Namen waren doch ganz rechtmässig veröffentlicht, so besonders die aufgrund der ukrainischen Flora geschaffenen Neukombinationen oder die meisten *Mentha*-Nothomorphen, auch Namen anderer ungarischer Autoren (z. B. *Veronica* × *Soóiana* Borsos 1967).

In dieser Abhandlung habe ich vor allem jene neue Taxa noch einmal aufgezählt, deren genauer Holotypus nicht erwähnt wurde, so dann jene Neukombinationen, die sich auf Arten, Unterarten oder Varietäten beziehen und bei denen die Basionyme von mir früher nicht vollständig mitgeteilt worden sind. Manche früher (meist in Bot. Közl.) nur provisorisch (ohne Basionyme) veröffentlichten Neukombinationen habe ich versäumt, in den Acta Bot. Hung. gültig zu publizieren, das wurde nur hier nachgeholt. Dagegen habe ich auf die Unzahl der von mir mitgeteilten Neukombinationen, die nur Formen oder Lusus bezeichnen, verzichtet, wenn sie auch »non rite publicata« sind. Es ist wirklich kaum von Bedeutung, wer der zweite Autor einer Form ist. In meiner Synopsis habe ich zwischen Varietät und Form, was den Autorennamen betrifft, keinen Unterschied gemacht und somit viele alte Varietäten als Formen bewertet, ohne den Autorennamen zu wechseln. (Sonst hätte ich noch einige hundert weitere Neukombinationen schaffen müssen.) Nur wenn ich ein nomen novum geben musste (meist wegen eines älteren Homonyms), ergänze ich hier das unvollständige Basionym.

So ist vorliegende Mitteilung ein Nachtrag und eine Ergänzung der Serie Species et combinationes novae florae Europae praecipue Hungariae I—X. (Acta Bot. Acad. Sci. Hung. **9** (1963) — **17** (1971).

Abbreviationes: Dscr.: descriptio, Ht: holotypus, Hb: Herbarium.

Biscutella laevigata L. ssp. *hungarica* Soó Acta Bot. Hung. **10:** 373 (1964) (Dscr.) Ht.: Bükk-Geb.: Bélkő (Soó Hb. Univ. Debrecen), cotypus: Vértes-Geb. »Fánivölgy: Faniental« (Soó, Hb. Horti Bot. Budapest) — ssp. *austriaca* (Jord.) var. *budensis* Soó l. c. (Dscr.) Ht.: Budaer-Geb. (MÜLLER): »Gellért-Berg« (HAYNALD), in Hb. Mus. Nat. Hung.

Valeriana Tripteris ssp. *austriaca* E. Walther var. *carpatica* Soó Acta Bot. Hung. **1:** 250 (1964) (var. *Hoppei* et *intermedia* auct. carp.) (Dscr.) Ht.: Siebenbürgen: Bihar (Bihor)-Geb.: Vidra (SIMONKAI Hb. Mus. Nat. Hung.).

V. officinalis L. var. *Sárkányii* Soó Acta **4:** 195 (1958)(A. et D. Löve 1961 p. ssp.) Ht.: Mittelungarn: Tabdi, l. BARANYAI, nach lebender Pflanze beschrieben.

V. sambucifolia Mikan ssp. *procurrens* (Wallr.) Soó var. *calvescens* (E. Walther Mitt. Thür. Bot. Ges. 1 (1949) Beih. 57 p. var. *V. procumbentis*) Soó Acta Bot. Hung. **11:** 250 (1961).

Succisella inflexa (Kluk) Beck f. *Beckii* Soó l. c. (Dscr.) Ht.: Bükk-Geb.: Miskolc-Tapolca (Soó Hb. Univ. Debrecen)

Nymphaea alba L. f. *csepelensis* Soó l. c. (Dscr.) Ht.: Csepel-Insel, in aqua fluvii Duna pr. Soroksár (Soó, Hb. Horti Bot. Budapest).

Alchemilla hungarica Soó l. c. 424 Dscr. in Palitz Acta Geobot. Hung. **1:** 116 (1936) et Soó Feddes Repert. **40:** 767 (1936) sub nomine »*A. plicata*«. Ht.: Bükk-Geb.: Lillafüred, Jávorkút (Soó Hb. Univ. Debrecen).

Euphorbia pannonica Host. var. *pulverulenta* (Kit.) Beck f. *Kitaibelii* Soó Acta Bot. Hung. **11:** 245 (1965) (Dscr.) Ht.: Balatonalmádi (Soó Hb. Univ. Debrecen).

Thymus glabrescens Willd. ssp. *Degenianus* (Lyka Bot. Közl. **20:** 147 p., 1922 ssp. *Th. Serpylli*) Soó Bot. Közl. **49:** 157 (1961) sine basionymo.

Th. × *Soói* Lyka (*Th. glabrescens* × *Degenianus*) in Soó Acta Bot. Hung. **12:** 121 (1966), Fragm. Flor. Geobot. **16:** 36 (1970) Ht.: Debrecen »Nagycsere, Haláp« (Soó Hb. Horti Bot. Budapest), cum nm. *nyirségensis* Soó l. c.

Astragalus asper Wulf. f. *Kárpátii* Soó Acta Bot. Hung. **12:** 355 (1966) (Dscr.) Ht.: Mittelungarn, Kom. Pest.: Dabas (Hb. Z. KÁRPÁTI).

Solanum Dulcamara L. var. *pusztarum* Soó l. c. 356 (Dscr.) Ht.: Mittelungarn, Kom. Bács-Kiskun: Bugacpuszta (Soó Hb. Horti Bot. Budapest).

Verbascum Lychnitis L. ssp. *Kanitzianum* (Simk. et Walz) Soó f. *Rochelianum* Soó l. c. 357 (Dscr.) Ht.: Ostkarpaten: Öcsém (Soó Hb. Univ. Cluj).

Cardamine hirsuta L. f. *apetala* Soó l. c. 363 Ht.: Bakony-Geb.: Cuhatal (Soó Hb. Univ. Debrecen).

C. amara L. f. *monochlamydea* Soó l. c. 363 Ht.: Bükk-Geb.: Jávorkút (Soó Hb. Univ. Debrecen).

Potentilla impolita Wahlbg. f. *Borbásiana* Soó l. c. 424 (Dscr.) Ht.: Debrecen (Soó Hb. Univ. Debrecen).

Rorippa silvestris (L.) Bess. ssp. *Kerneri* (Menyh.) Soó f. *Olgae* Soó l. .c. (Dscr.) Ht.: Kom. Hajdú: Hortobágy (Borsos Hb. Univ. Debrecen).

Polygala amarella Cr. var. *salsa* Degen ex Soó Acta Bot. Hung. **13:** 300 (1967) (Dscr.) Ht.: Csepel-Insel: Szigetcsép et Szigetszentmiklós (Degen Hb. Mus. Nat. Hung.).

Origanum vulgare L. ssp. *barcense* (Simk.) Jáv. f. *chlorescens* Simk. ex Soó-Borhidi Annal. Univ. Budapest. Sect. Biol. **9—10:** 361 (1968) Ht: Südkarpaten: Königstein: Királykő, Propasta (Simonkai Hb. Mus. Nat. Hung.).

Senecio paludosus L. f. *gymnocarpus* Soó Acta Bot. Hung. **13:** 308 (Dscr.) Ht.: Kom. Pest: Ócsa (Soó Hb. Bot. Budapest) — var. *tomentosus* (Host.) Koch f. *hungaricus* Soó l. c. (Dscr.) Ht.: Kom. Pest: Bugyi (Soó Hb. Univ. Debrecen).

Sonchus asper (L.) Hill. var. *pungens* Bischoff f. *adenotrichus* Soó Acta Bot. Hung. **14:** 152 (1968) (Dscr.) Ht.: Debrecen, in ruderatis (Soó Hb. Univ. Debrecen).

Erophila verna (L.) Chevall. ssp. *microcarpa* (Wibiral) Oberd. var. *hungarica* Borsos et Soó Acta Bot. Hung. **14:** 404, 408 (1968) (Dscr.) Ht.: Szentendreer Geb.: Pomáz »Kiscsikóvár« (Degen, Hb. Mus. Nat. Hung.), cotypus: Bükk-Geb.: Eger »Mészhegy« (Vrabélyi Hb. Mus. Nat. Hung.) — var. *vértesensis* Borsos et Soó l. c. (Dscr.) Ht.: Vértes-Geb.: Vértesboglár (Boros Hb. Boros).

Salicornia prostrata Pall. ssp. *Simonkaiana* Soó Acta Bot. Hung. **15:** 341 (*S. Simonkaiana* Soó l. c. **6:** 401, 1960 p. sp., dscr.) Ht.: Budapest »Lágymányos« (Simonkai Hb. Mus. Nat. Hung.).

Allium vineale L. l. *virescens* Soó Acta Bot. Hung. **16:** 365 (Dscr.) (*A. v.* var. *virens* A. et Gr. Syn. III: 110, 1905 non Boiss. Fl. Or. **V:** 236, 1884).

Coeloglossum viride (L.) Hartm. f. *integrum* Soó l. c. (Dscr.) [*C. v.* var. *islandicum* M. Schulze Öst. Bot. Zschr. **48:** 113 (1898) quoad pl. helveticam: Feegletscher, leg. Jaccard. non *Peristylus islandicus* Lindl.]

Ophrys exaltata Ten. ssp. *Sundermannii* Soó Acta Bot. Hung. **16:** 392 (1970) (*O. biscutella* Danesch Orchidee **21:** 357, 1970) (Dscr.) Ht.: Italia, mt. Gargano (Sundermann Hb. Mus. Wuppertal).

O. fuciflora (Cr.) Sw. var. *cornigera* (Beck) A. et G. f. *Tallósii* Soó Acta Bot. Hung. **5:** 457 (1959), var. *intermedia* Moggr. f. *triloboviridis* Soó l. c. (Dscr.) Ht.: Bakony-Geb.: Devecser »Széki-erdő« (Tallós Hb. Horti Bot. Budapest).

O. Chatenieri Rouy nm. *bakonyensis* Soó l. c. 469 (*O. fuciflora* var. *cornigera* × × *O. sphegodes* var. *fucifera*) (Dscr.) Ht.: ibidem.

Festuca Wagneri Degen, Thaisz, Flatt var. *hungarica* Soó Acta Bot. Hung. **9:** 431 (1963) (*F. stricta* Host var. *hungarica* Soó l. c. **2:** 199 1955 dscr.) Ht.: Budapest: Rákos (DEGEN Gram. Hung. 179 sub *F. glauca* var. *scabrifolia*, Hb. Mus. Nat. Hung.) Cotypus: Csepel (SIMONKAI Hb. Mus. Nat. Hung.), — f. *Horánszkyana* (Soó 1955 l. c. dscr.) Soó Acta l. c. Budapest: Káposztásmegyer (HORÁNSZKY Hb. Univ. Budapest).

Fraxinus angustifolia Vahl ssp. *pannonica* Soó et Simon Acta Bot. Hung. **6:** 148 (1960) (Dscr) Ht.: Mittelungarn: Ócsa (Soó Hb. Horti Bot. Budapest), Cotypi: Bugyi (BOROS Hb. BOROS), Rumänien, Dobrogea: Letea (SIMON Hb. Horti Bot. Budapest).

Scabiosa × *Janchenii* Soó Acta Bot. Hung. **11:** 251 (1965) Dscr. *S. Columbaria* × *ochroleuca*, Melzer Verh. Zool. Bot. Ges. 1955: 95.

S. ochroleuca L. f. *Baumgarteniana* Soó l. c. 250 (Dscr.) Ht.: Siebenbürgen: Kolozsvár-Cluj »Szénafű« (Soó Hb. Univ. Cluj).

Adenophora liliifolia (L.) Bess. var. *Pócsii* Soó Acta Bot. Hung. **4:** 197 (1958) (Dscr.) Ht.: Mittelungarn: Kom. Pest: Sári (PÓCS Hb. Horti Bot. Budapest).

Caltha palustris L. ssp. *laeta* (Sch., Nym., Ky.) Hegi f. *transsilvanica* Soó et Kovács-Láng Ann. Univ. Budapest. Sect. Biol. **8:** 339 (1966) (Dscr.) Ht.: Siebenbürgen, Kom. Hunyad: Nozság-Vormaga (SIMONKAI Hb. Mus. Nat. Hung.) — f. *retyezatensis* Soó et Kovács-Láng l. c. Ht.: Siebenbürgen: Retyezát-Geb., Zenoga-See (JÁVORKA Hb. Mus. Nat. Hung.) — f. *Simonkaiana* Soó et Kovács-Láng l. c. 340 Ht.: Siebenbürgen: Erzgebirge »Csáklyaikő« (SIMONKAI Hb. Mus. Nat. Hung.) — ssp. *cornuta* (Sch., Nym., Ky.) Hegi f. *platycarpa* Soó et Kovács-Láng l. c. Budapest: Óbuda-Aquincum (BOROS Hb. BOROS) — f. *arrabonensis* Soó et Kovács-Láng l. c. Kleine Ungar. Tiefebene: Győrszentjános (POLGÁR Hb. Univ. Debrecen).

Aquilegia vulgaris L. var. *Soói* É. Kovács Ann. Univ. Budapest. Sect. Biol. **8:** 306 (1966) (Dscr.) Ht.: Budaer Geb. Pilisszentiván: »Kis- u. Nagyszénáshegy« (Soó Hb. Univ. Debrecen), Cotypi: ibidem (JÁVORKA Hb. Mus. Nat. Hung., BOROS Hb. BOROS) — Vielleicht mit subsp. *nigricans* (Baumg.) var. *Ebneri* Beck identisch.

Trifolium arvense L. f. *Komlódiae* Soó l. c. **8:** 313 (1966) (Dscr.) Ht.: Börzsöny-Geb.: Szokolya (BOROS Hb. BOROS).

Rhinanthus gracilis Schur ssp. *Stojanovi* Soó Izv. Bot. Inst. Bulg. Akad. **6:** 368 (1958) (Dscr.) Bulgarien, Rila-Geb.: Borovez »Sokolec« (SIMON Hb. Horti Bot. Budapest).

Dactylorhiza × *Vermeuleniana* Soó (*majalis* × *maculata*) Jb. Naturw. Ver. Wuppertal **21—22:** 17 (1968) Dscr.: VERMEULEN Fl. Neerl. I. **5:** 89 (1959) sub *D. Braunii* (Hal.) Soó, quae est *D. majalis* × *fuchsii*.

Anchusa Barrelieri (All.) Vitm. lus. *Péterfii* Soó Acta Bot. Hung. **12:** 356 (1966), *Digitalis grandiflora* Mill. f. *Péterfiana* Soó l. c. **13:** 303 (1967), *Melam-*

pyrum bihariense Kern. l. *devanum* Soó l. c. Ht.: alle Siebenbürgen: Déva (Péterfi Hb. Univ. Cluj). Die weiteren Holotypi der von mir beschriebenen neuen Lusus teile ich nicht mit, ich halte das für unbedeutend, da solche Farbenabarten überall auftreten können.

Batrachium × *virzionense* (Félix Bull. Soc. Bot. France **59:** LXIII, 1912 (1913) sub *Ranunculo*) Soó Acta Bot. Hung. **9:** 422 (1963) (*B. aquatile* × × *radians*).

B. × *Glückii* Soó l. c. = *B.* × *lambertii* (Félix l. c. *Ranunculo*) Soó Acta Bot. Hung. **13:** 299 (1967) (*B. aquatile* × *Baudotii*).

B. × *Cookii* Soó l. c. (*Ranunculus* × *Glückii* Félix et Cook Mitt. Bot. Staatss. **6:** 202 (1966) non *B. Glückii* Soó 1963, *B. Félixii* Soó 1966 non Segret 1925 (*B. circinatum* × *trichophyllum*).

B. × *Segretti* (Félix l. c. sub *Ranunculo*, 1913) Soó l. c. (*B. Baudotii* × *trichophyllum*).

Pulsatilla grandis Wender. f. *Borbásiana* Soó Acta Bot. Hung. **9:** 421 (1963) (var. *angustisecta* Neilr. Fl. Nied. Öst. 1859. 674 non Rchb. 1840).

P. grandis Wender. f. *pseudoslavica* Soó l. c. (Dscr.) Ht.: Tornaer Karst »Szelcepuszta« (Soó Hb. Univ. Debrecen).

P. Jankae (F. Schultz) Schur var. *australis* Soó l. c. = *P. Jankae* var. *Jankae* (*P. montana* ssp. *dacica* Rummelspacher 1965) non *P. australis* (Heuff.) Soó comb. n. (*Anemone Pulsatilla* var. *australis* Heuff. Verh. Zool. Bot. Ges. **8:** 42, 1858.)

Malus silvestris (L.) Mill. ssp. *paradisiaca* (L. Sp. pl. 1753: 479 p. var. *Pyri Mali*) Soó l. c. 423 (1963).

Crataegus × *Uhrovae* Soó Acta Bot. Hung. **11:** 237 (1964) Dscr.: *C. curvisepala* × *Oxyacantha* Hrabětová-Uhrová Biológia **13:** 788 (1958).

C. monogyna Jacq. var. *Tauscheri* (Gandoger ap. Kern. Monatschr. f. Preuss. Gartenbau 1875: 185) Soó l. c. 237 (1964).

Cerasus avium (L.) Mönch convar. *duracina* (L.) Janch. var. *albida* (Ehrh. Beitr. Naturk. **7:** 128, 1792 p. var. *Pruni variae*) Soó l. c. 239.

Ribes Uva-crispa L. ssp. *hunyadensis* (Simk. Bot. Közl. **8:** 24, 1909 p. var. *R. Grossulariae*) Soó Acta Bot. Hung. **9:** 426 (1963).

Sempervivum marmoreum Gris. ssp. *blandum* (Schott) Soó f. *pallidiflorum* Soó Acta Bot. Hung. **9:** 426 (1964) (*S. Schlehani* var. *genuinum* Domin Rozpr. II. tr. České Akad. XLII: no. 29, p. 34 cum diagn.).

Anthriscus Caucalis M. B. var. *gymnocarpa* (Moris Flora Sardoa **2:** 235, 1843) Soó Acta Bot. Hung. **11:** 243 (1964).

Libanotis pyrenaica (L.) Bourg. ssp. *athamanthoides* (Spr. Plant. Umbell. Prod. 1843, 40 sub *Ligustico*) Soó l. c. 244.

Heracleum Sphondylium L. ssp. *flavescens* (Willd. Spec. pl. ed. 4. **I:** 1421 (1797) p. sp.) Soó Bot. Közl. **50:** 191 (1963), Acta l. c. 245 sine basionymo (*H. sibiricum* auct. eur).

Glechoma hederaceum L. ssp. *sardoum* (Béguinot Nuovo Giorn. Bot. Ital. **19:** 578 p. sp.) Soó Acta l. c. 248.

Calamintha officinalis Mönch ssp. *subnuda* (W. et K. Pl. rar. Hung. III: 291, 1810 sub *Melissa*) Soó Acta l. c. 249.

Caltha palustris L. ssp. *laeta* Hegi var. *Borbásii* Soó Acta Bot. Hung. **12:** 111 (1966) (var. *truncata* Beck Verh. Zool. Bot. Ges. **36:** 349 1886 non Peterm. 1838) — f. *czarnohorensis* (Zapał. Consp. Gl. Gal. **2:** 186, 1908 p. var. *C. laetae*) Soó et Kovács-Láng Ann. Univ. Budapest Sect. Biol. **8:** 339 (1966).

Ficaria verna Huds. ssp. *bulbifera* A. et D. Löve f. *divergens* (F. Schultz Arch. II. 122, 1855 sub *Ranunculo*) Soó Ann. Univ. Budapest. Sect. Biol. **8:** 298 (1966), f. *dolichopetala*, f. *polypetala*, f. *podolica*, f. *elongata* (Zapał Consp. Fl. Galic. **2:** 258 sub *Ranunculo*) Soó l. c.

Rosa × *Schwertschlageri* Soó Acta l. c. 115 (*canina* × *rubiginosa*) Dscr. Bez. Bayr. Bot. Ges. **11:** 171 (1907); KELLER: Syn. Ros. Eur. Mediae 530 (1931)

Pimpinella Saxifraga L. var. *procera* (Weide Feddes Repert. **88:** 268 p. ssp, 1962) Soó Acta Bot. Hung. **12:** l. c. 116.

Cruciata pedemontana (Bell.) Ehrend. var. *vestita* (Rouy Fl. Fr. **8:** 7, 1903 sub *Galio*) Soó Acta 355 (1966).

Galium humifusum M. B. ssp. *cincinnatum* (Klokow Fl. URSR. X. 108, 455 1961 pro *Asperula cincinnata*) — ssp. *Besserianum* (Klokow l. c. 111, 456 pro *A. Besseriana*) Soó l. c. 117.

G. boreale L. f. *exoletum* (Klokow l. c. 185, 460) — *G. rubioides* L. f. *pseudoboreale* (Klokow l. c. 185, 460) Soó Annal. Univ. Budapest. Sect. Biol. **9—10:** 378—379, (1968).

Galium glaucum L. var. *hirsutum* (Wallr. Sched. crit. 60, 1822 p. var. *A. galioidis*) Soó Bot. Közl. **49:** 155 (1961) sine basionymo.

Althaea officinalis L. ssp. *pseudoarmeniaca* (Polgár Bot. Közl. **38:** 291, 1941, p. var.) KÁRPÁTI ex Soó Acta l. c. 119.

Die *Mentha dumetorum* Schult. und *M. dalmatica* Tausch Neukombinationen (Soó Acta l. c. 122—123) sind als Varietäten zu bewerten. Wenn wir aber diese Arten als hybridogen betrachten, so müssen wir die Varietäten als Nothomorphen bezeichnen. Somit sind meine Kombinationen eindeutig.

Arctium nemorosum Lej. et Court. f. *Máthéi* Soó l. c. 308 (var. *microcephalum* (Wilpert Mon. *Arctium* 1928 sub *A. pubente*) Máthé Acta Geobot. Hung. **1:** 233, 1937 non Erdner 1904 sub *Lappa*).

Centaurea macroptilon Borb. ssp. *oxylepis* (W. et Gr. Fl. Sil. 107 p. subvar. *C. jaceae* var. *ciliatae*, 1829) Soó Acta Bot. Hung. **4:** 197 (1958).

C. Scabiosa L. var. *coriacea* (W. et K.) Koch f. *Dostálii* Soó Acta Bot Hung. **13:** 309 (1967) (f. *calvescens* sf. *homoephylla* Dostál Publ. Fac. Sc.

Univ. Charles, no. 160 (1938): 18 non W. et Gr.), f. *subheterophylla* Soó l. c. (sf. *variifolia* Dostál l. c. non Loisl.).

Cirsium vulgare (Savi) Ten. ssp. *silvaticum* (Tausch) Arènes f. *Erdneri* Soó Acta Bot. Hung. **13:** 309 (1967) (var. *oligocephalum* Erdner Fl. Neuburg 1911: 500 non Schur 1866).

Crepis capillaris L. var. *agrestis* (W. et K.) D. T. et Sarnth. f. *integra* (Bischoff Cichoriaceen 1851: 277 sub *C. virente*) Soó Acta Bot. Hung. **14:** 153 (1968), f. *Bischoffii* Soó l. c. (*C. virens* var. *diffusa* Bischoff l. c. non DC.).

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Ulmus minor Mill. var. *suberosa* Soó Bot. Közl. **51:** 231, 1964 sine basionymo: var. *suberosa* (Mönch Verz. Weissenstr. 1785: 1363 p. sp.) Soó.

Carex × *Senayana* Soó Acta Bot. Hung. **9:** 371 (1970) (*C. cuprina* (»*Otrubae*«) × × *spicata*) (*C. Haussknechtii* Senay Bull. Hist. Nat. Mus. Paris ser. 2. **17:** 447, 1945 non Podp. 1929).

Orchis × *Gennarii* Rchb. f. nm. *Popii* Soó Rev. Roum. Biol. **12:** 226 (1967) (*O. Gennarii* auct. rumen. Dscr. in Panţu Orchidaceele din România 1915: 39) (*O. papilonacea* × *O. Morio* ssp. *picta* var. *caucasica*).

Pinus silvestris L. ssp. *pannonica* (Schott Forstw. Centralbl. **29:** 1907: 212) Soó Bot. Közl. **49:** 147 (1961) sine basionymo.

Dryopteris dilatata A. Gray var. *dumetorum* (Sm. Engl. Fl. IV: 281, 1828 sub *Aspidio* p. sp.) — var. *Chanteriae* (Moore Ferns Gr. Brit. 1855 pl. 24 p. — var. *Lastraea dil.*) — var. *collina* (Newm. Nat. print. Ferns: 224, 1855 p. var. *Lastreae dil.*) Soó Acta Bot. Hung. **10:** 369 (1964) sine basionymis.

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SEXUAL CORRELATION IN SELF-COMPATIBLE AND SELF-INCOMPATIBLE VARIETIES OF SOME PRUNUS

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Investigations of flowers of various self-compatible and self-incompatible *Prunus* taxa showed that pistil length in the former varieties is greater than in the latter within the same species. Contrarily, stamen number of self-incompatible plants is greater than that of self-compatibles; the quotient of stamen number and pistil length shows a significant difference between the autofertile and autosterile varieties of the several species.

A verified negative correlation exists between pistil length and stamen number in cultivated *Prunus* species. This relationship differs in the self-compatible and in self-incompatible varieties, and the quotient renders the difference between the two forms more conspicuous.

Introduction

Among cultivated *Prunus* species both self-compatible and self-incompatible varieties can be found. *Armeniaca vulgaris* is generally self-compatible, whereas *Armeniaca mume* and *Armeniaca ansu* are self-incompatible (Kostina 1964). As far as known no male sterility has been found in apricots, while female sterility is quite frequent. Schröder (1928) and Schanderl (1932) reported abnormal pistils in the flowers of certain apricot varieties. This observation was confirmed later by Maliga (1947), who also observed that more flowers with rudimentary pistil developed in the upper part of the crown and water shoots than in the under part of the crown and on older feathers.

Within *Prunus domestica* several self-compatible varieties occur, but there are well-known self-incompatible types as well. The varieties 'Besztercei' and 'Vörös szilva' are mainly self-compatible. However, 'Esperen Goldpflaume' and 'Datolyaszilva' are male sterile, there is no pollen in the anthers (Kobel, 1954). Female sterility may occur as well. Very probably this is the cause of the self-incompatibility found in the varieties 'Alutscha' and 'Késői muskotályszilva' (Tóth, 1967). 'Kirkes pflaume' is a curiosity, as it can have 3—5 pistils in one flower, yet it cannot be fertilized by its own pollen (Porpáczy et al., 1964).

In most forms of *Persica vulgaris* there are no importent barriers against pollination. Disturbances in pollen development resulting in male sterility were observed by Connors (1922) on 'I. H. Hale', by Knowlton (1924) on 'Late Grawford' and by Kerr (1927) on 'Juny Elberta'. As for some other

varieties, MOHÁCSY—MALIGA—MOHÁCSY Jr. (1963) mention self-incompatibility in 'Chinese Cling' and 'Sargents Chinese Peach'. ALDERMAN's (1926) report deserves special interest: he obtained hybrids lacking pistils when crossing the species *Amygdalus nana* with *Persica vulgaris*.

Self-incompatibility is more common in sweet and sour cherries, but sterility caused by morphological aberrations are hardly found. Some such related species are not fruit-bearing, but ornamental trees, e.g. *Cerasus serrulata* and *Cerasus vulgaris* cv. 'Plena'. According to KOBEL (1954), sweet cherry is completely self-incompatible, while MOHÁCSY—MALIGA (1956) consider the early varieties 'Früheste des Marktes' and 'Frühe Mai' self-compatible. In the sour cherry varieties there are more self-compatible varieties, in an essentially higher percent. Thus, 'Grosser Gobet', 'Schöne von Chatenay', 'Bigarreau de Montreuil' are selfcompatible, while 'Kentish Red', 'Bing', 'Pándy üveg-meggy', 'Ostheimer Weichsel', etc. are self-incompatible (KOBEL, 1954 and MOHÁCSY—MALIGA, 1956).

The development of the flower organs is genetically determined. A great number of reports deal with the correlation between stamens and pistils, but they are delimited in essence to a few species (RUHLAND, 1967). There is no mention in that work whether morphological self-incompatibility can be inferred from the morphology of the flower organs. KOBEL (1954) does not hold it possible: "We cannot tell by the flower structure for instance that almond varieties are self-incompatible and peach varieties self-compatible (... so lässt sich beispielweise aus den Blütenbau nicht erkennen, dass die Mandelsorten selbststeril, die Pfirsichsorten dagegen selbstfertil sind . . .). We cite him word by word because according to our investigations distinct differences can be found between varieties of self-compatible and self-incompatible plums, sweet and sour cherries. The ratio termed "flower-index" — stamen number for unit style length — proved suitable to demonstrate also the difference between self-compatible and self-incompatible species.

The present paper discusses the correlation between the pistils and stamens of various self-compatible and self-incompatible varieties differing in the quotient. Presumably the difference in sex correlation in self-compatible and self-incompatible varieties is responsible for the higher quotient of the self-incompatibles than that of the self-compatibles and the stamen number related to the entire pistil may render an even more reliable index.

Material and method

Our investigations at Cegléd involved the self-compatible 'Rose apricot C. 778', the peach variety 'Champion', the plum 'Besztercei', the sweet and sour cherry varieties 'Früheste des Markets' and 'Bigarreau de Montreuil', as well as the self-incompatible *Armeniaca ansu*, the self-incompatible *Armeniaca ansu*, the peach 'I. H. Hale', the plum 'Jeruzsálemi kék' and

cherries 'Grosser Germersdorfer' and 'Ostheimer Weichsel'. The average age of the trees was 15 years. Ten flowers each were picked from 2 trees of every variety. In the 20 flowers per variety the length of the pistil was measured, the respective stamina counted and from the two data the quotient calculated. Differences between the mean values were examined by variance analysis.

From pistil length and stamen number correlations were calculated in the self-compatible and self-incompatible varieties. We examined first whether a correlation can be found between the two flower organs (x^2-test). As a significant correlation appeared the correlation coefficient r-value was calculated for a simple linear regression by the data of 100 flowers each.

In the correlation curve thus obtained, stamen number was read between the 12—19 mm pistil length range (92 per cent of the data within this range). Thus corrected quotient values were received. Referred to self-compatible and self-incompatible *Prunus* varieties this necessitated another variance analysis to explain the deviation in magnitude of the quotient thus obtained.

Results

The pistil length of self-compatible *Prunus* varieties shows characteristically greater means than that of self-incompatible ones (Table 1). The results proved also significant with the exception of the two sour cherry varieties compared. At the same time, the self-incompatible varieties have relatively more stamina compared to the self-compatible ones, but this could not be proved between the sweet cherry varieties 'Früheste des Marktes' and 'Grosser Germesdorfer'. Accordingly, the quotient of stamen number and pistil length is significantly smaller in self-compatible varieties than in the self-incompatible ones.

Table 1

The pistil-length, the stamen-number and the quotient by five self-compatible (1) and self-incompatible (2) varieties of some Prunus

Self-compatible (1) Self-incompatible (2)	Pistil-length, mm	Stamen-number, pc	Quotient pc/mm
'Besztercei' (1)	16.55**	20.19	1.22
'Jeruzsálemi kék' (2)	12.95	29.95***	2.31***
Champion (1)	15.50*	32.55	2.10
I. H. Hale (2)	14.31	33.63*	2.35*
Rose apricot C778 (1)	17.35**	29.00	1.67
Armeniaca ansu (2)	11.35	30.15*	2.66**
Früheste des Markt (1)	14.15*	37.07	2.62
Grosse Germersdorfer (2)	13.30	37.51	2.82*
Bigarreau de Montreuil (1)	12.83	35.15	2.74
Ostheimer Weichsel (2)	12.55	36.52*	2.91*

* p = .05
** p = .01
*** p = .001.

The correlation between pistil length and stamen number was examined by the x^2-test in self-compatible and self-incompatible *Prunus* species, individually. In the self-compatible varieties and according totheritical values published by WEBER (1964), the connection is significant at the 0.1 per cent level ($x^2 = 156.8$ and FG = 98). The correlation is similar in the self-incompatible varieties as well ($x^2 = 141.3$ and FG = 98). The correlation between the male and female sex organs may therefore be regarded as linear and the variation in the stamen number depending on pistil length could be demonstrated successfully also in this way. According to the graph in Figure 1, the variation in stamen number is much greater in the self-compatible varieties than in the self incompatible ones. At the same time, the variability of pistil length is practically the same in both types.

Already by our previous observations, the correlation effect between the gynoecium and the androecium is assumable behind the flower-index. The flower-index, elaborated by us, indicates namely the relative condition which leads to self-incompatibility when morphological anomalies are present. The average pistil length in self-compatible and in self-incompatible varieties falls generally between 12—19 mm (92 per cent of data), therefore from the regression analysis curves within this range, corrected stamen numbers belonging to whole values could read. From the results thus obtained, the quotients were calculated, on which variance analysis was made. The quotient involving the correlation effect shows a distinct deviation when comparing self-compatible and self-incompatible *Prunus* varieties (Table 2). The table shows

Table 2

The pistil-size and the quotient of stamen-number and pistil-length in average values of self-compatible and self-incompatible Prunus varieties

Replications	Pistil-length, mm	Quotient, pc/mm Self-compatible and Self-incompatible varieties	
1.	12	3.05	2.86
2.	13	2.63	2.59
3.	14	2.08	2.36
4.	15	1.83	2.15
5.	16	1.68	1.97
6.	17	1.44	1.82
7.	18	1.26	1.68
8.	19	1.11	1.56
Average		1.88	2.12*

* Significantly greater than the self-compatible varieties at 5 per cent level

every repetition; a distinct deviation from the above statement was found only at the 12 mm pistil length. However, this pistil length occurred in a frequency of merely 3—4 per cent in the material.

The difference in correlative effect found between the gynoecium and the androecium in the flowers of self-compatible and self-incompatible *Prunus* varieties indicates that the relationship between the male and female organs cannot be neglected in fruit-bearing trees. The quotient indicates that sterility resulting from morphological characters can be predicted also by the flower
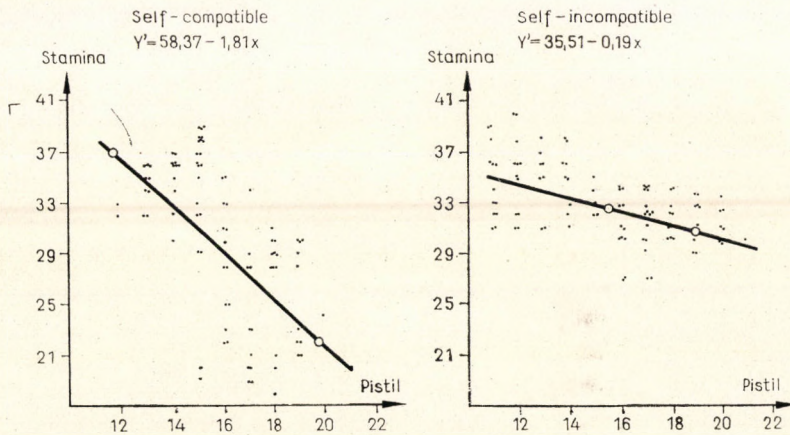
Fig. 1. Linear regression of pistil-length and of stamen-number by self-compatible (1) and self-incompatible (2) *Prunus* varieties. A significantly connection at 0.001 level: (1) — $r = -0.619$, (2) — $r = -0.400$

organs. Of course, for the moment it is true only for the given extreme cases, but, according to other experiments, the quotient could be adequately used to characterize the relations of fertility. The first approach to show the correlative effect was based on the stamen number for unit style length presumable adequately characterizing sex correlations (SURÁNYI, 1971a). It is, however, more reasonable to take into account the whole length of the pistil. The original designation is likely to cause trouble, therefore the index to show correlative effect was named quotient.

Discussion

The longer pistil of the self-compatible varieties implies that flower, considered as a modified shoot, supresses the numerical increase of stamina which be taken for lateral branches (GIMESI, 1954). Accordingly, more stamina as related to a shorter pistil can be found in self-incompatible flowers.

The demonstrable negative correlation between pistil and stamina suggest that the interrelation of growth regulators determines the different organization of flower organs. The sexual character is genetically fixed in every flower typ (CATARINO, 1964), but growth regulators can be involved in the mechanism through additive genes (RESENDE, 1967). This is the explanation of the sex changing or modifying effect of several hormones and mechanical treatments (pruning, ringing, defoliation and abscission of flowers) (RUHLAND, 1967).

According to a great number of literary data, a relatively high auxin level is favourable to the gynoecium, while the development of stamina requires a lower auxin level (RUHLAND, 1967). If we consider that in flowers the vegetative character decreases in the direction calyx → gynoecium → corolla→ androecium (RESENDE, 1967), then the organization of shoots as well as the formation of pistil and stamina may also be connected by means of the general hormone regulation, e.g. different flower types depend on internode. Our experiments seem to support this suggestion. The internode length of one year old shoots fine varieties with more stamina was significantly shorter than varieties of the same species with fewer stamina and a longer pistil (the examined varieties had an identical rootstock!) (SURÁNYI, 1971b).

It would be desirable to increase the number of self-compatible and self-incompatible *Prunus* varieties, and to determine the optimum range of the quotient, because further unambiguous results could render this ratio useful in breeding when making a positive selection for self-compatibility. On the other hand, the work initiated here to examinate sex correlations would lead to a better cognition of the hormone interrelations involved in the organization of flowers and to reduce or eliminate the sterility in self-incompatible varieties by hormone treatments.

Acknowledgement

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THE EFFECT OF ARCTIINE ON GERMINATION, ON ROOT TISSUES AND ON NUCLEIC ACIDS

By

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This paper consists of three parts. A: Further data are furnished on the relation between the annual rhythm of germination and the arctiine content; the arctiine content of the various organs is examined and a relation between the arctiine content and the *Compositae* flower-type is established. B: In the second part the effect of arctiine on root tissues is demonstrated by histological examinations. No substantial effect due to arctiine can be observed in the tissues of the stem. C: The interaction of arctiin with nucleic acids is demonstrated by circular dichroism. In the presence of arctiine the conformation (into a double helix?) of the nucleic acids changes markedly.

In a previous paper (SZABÓ, GARAY 1970) it was pointed out that arctiine inhibits the germination of various plants. The question, however, whether this effect manifests itself at a histological level, or, more exactly, what tissue element of the stem and the root are sensitive to arctiine, was not investigated. No mention was made about the effect of arctiine on macromolecules, although there are some data on the interaction between nucleic acids and phenolics. According to D'AMATO and HOFFMAN–OSTENHOF (1956), ortho- and para-phenols exert a mutagene effect in plants. CHAJLAHJAN (1961) remarks that in the effect of gibberellins on nucleic acids cinnamic acid plays a roll. Growth stimulation induced by cumarin appears also on the RNA level (KNYPL 1966). It is not known to the authors whether the interaction between plant phenolics and nucleic acids has been examined *in vitro*. The question, however, is justified, since according to the present theory the substances regulating the growth and organization probably act on the level of the nucleic acids.

Material and methods

Arctiin and arctigenin has been determined as described previously (SZABÓ, GARAY 1970). The seeds were germinated in Petri dishes on wet filter paper, and with 5 mg/ml arctiine solution, respectively. Germination took place in an incubator at 4000 lux, 14000–16000 erg/sq. cm, at 24°C. Three to seven days old seedlings were fixed and preserved in 50 per cent alcohol. The pieces of root and hypocotyl were embedded in celloidine. Cutting was carried out with a sliding microtome. After removing the celloidine, the slides were treated with a solution of 5–10 per cent sodium-hypochlorite and 2 per cent acetic acid. Then they were stained with Erlich-type acidic haemotoxyline, while those from which celloidine had not been removed were stained with gentiana violet. Evaluation was based on about 750 slides.

Four nucleic acids of different origin (yeast, y-RNA, Merck; t-RNA, Calbiochem; and highly polimerized p-RNA, Calbiochem;) were used for the investigation of interaction between arctiine and nucleic acids. The investigated DNA was prepared from blood of chicken embryo.

Unfortunately, there was no opportunity for studying the interaction between plant nucleic acids and arctiine. The nucleic acids were dissolved in ion-exchanged water (pH 6—6.5) containing 0.01 M NaCl, while the arctiine in ion-exchanged water. Measurements were carried out at room temperature, with Jasco-type ORD/UV-5 spectrophotometer equipped with CD attachment.

To determine whether arctiine acts through nucleic acids, the following experiments were carried out. The absorption and CD spectra of four different nucleic acids and of arctiine were taken. Then arctiine was mixed with the individual nucleic acids. After half an hour the absorption and CD spectra were again plotted, to check whether some kind of interaction between arctiine and nucleic acids had happened? In the absence of interaction we would obviously get spectra composed of the 2 individual spectra by simple addition i.e. (NS) + (A) = = (NS + A). If arctiine and nucleic acid enter into any kind of interaction, the CD spectra — which are extremely sensitive to various conformations — should differ from the sum of spectra taken separately.

Results and discussion

(*a*) *New data on the effect of arctiine on germination and its occurence in the various organs*

It has already been suggested in the previous paper that there is a connection between the arctiine content and the annual rhythm of germination in light and in darkness. The investigations had been prolonged for another year and so it was observed that there is a parallelism in the change of the arctigenine content of the ethanol-soluble fraction and the annual rhythm of germination. The higher percentage of germination observed in autumn and in spring is associated with the rise in the arctigenine content of the ethanol-insoluble fraction. However, the effect is not entirely definite. The ethanol-insoluble fraction gradually decreases with the annual changes of germination. The lowest values were recorded during the intensive spring germination (Fig. 1).
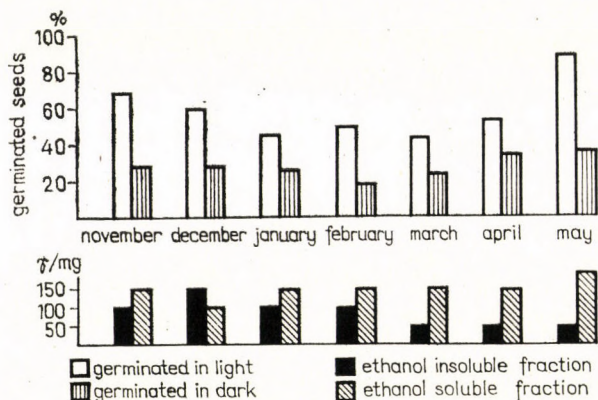
Fig. 1. Annual rhythm of germination of *Arctium lappa* as a function of arctigenine content of the seeds

The arctiine content of the organs of *Arctium lappa* was examined. As seen in Table I the occurence of arctiine is restricted to the inflorescence and the seed. It is interesting from chemotaxonomical point of view that there is connection between the *Compositae inflorescens*-type and the occurence of arctiine. No arctiine could be demonstrated in plants whose inflorescence axis is elongated (Table II) similarly as in the case of *Matricaria*-type inflorescence.

Table 1

Arctigenine content of Arctium lappa

Organs		Ethanol soluble	Ethanol insoluble
Leaf		—	—
Stem		—	—
Root		—	—
Seed		***	*
Full inflo-rescence	young	*	—
	old	***	—

Table 2

Inflorescence type and arctigenine content within the Compositae

Type of inflorescence	Species	Ethanol soluble	Ethanol insoluble
	Arctium lappa	***	**
	Arctium tomentosum	***	**
	Senecio cruentus	***	—
	Helianthus annuus	***	*
	Lactuca sativa	—	**
	Onopordum acanthium	***	—
	Tagetes patulus	*	**
	Zinnia elegans	***	—
	Carthamus tinctorius	—	—
	Bidens tripartitus	—	—
	Callistephus chinensis	—	—

(*b*) *The effect of arctiine on the morphology and tissue structure of seedlings*

The 5 mg/ml arctiine solution had an effect on all of the examined species. The size of the treated seedlings in comparison with the control seedlings became twice to three times smaller (Plate I). A similar inhibition manifested itself also in *Arctium lappa* seedlings despite the high endogene arctiine content of its seed.

Though the longitudinal growth of root was inhibited, arctiin had no effect on the shape and thickness of the root. Form remained also unchanged, while fewer and shorter radicals grew. The inhibiting effect of arctiine was manifest also in the epiblema formation. It can be stated — although no statistical examinations were carried out — that in the unit area of absorbing zone the number of root hairs is smaller and the hairs are shorter.

In 3—7 day-old arctiine-treated seedlings the shortening of the hypocotyl could still be observed.

For the examinations of the stem only hypocotyl pieces of a few mm length were at our disposal. No essential deviation could be observed in their tissue structure. Minimal deviations — apparent in the cell dimensions of phloem parenchyma, in the thickness of phloem, and in the change in shape of the starchy capsule cells — were found only in *Phaseolus*.

Concerning the roots arctiine caused changes only in the primary phloem and in the morphology of the root hairs. The endodermis often became polycellular and disarranged (Pictures 1 and 2, Plate II). The epiblasts of phloem parenchyma in *Cucumis* rapidly aged. Suberose-walled many-layered protective tissue appeared often on the whole surface, sometimes even on the top, in a few days. The intensive suberification is observable also on the young radicles. In certain areas this reaches such an extent that a destroying effect of the arctiine can be claimed (Pictures 3—5 in Plate II). This is confirmed also by the fact that no epiblema can be seen on the *Cucumis* roots.

Arctiine disturbed the normal activity of trichoblasts in the *Phaseolus*, *Arctium* and *Lactuca* species. It was frequently observed that on the same rhizodermal cell several root hairs were induced (Picture 3, Plate III).

The root hairs are extremely varying (Pictures 2—4 and 5, Plate III; Pictures 1—6, Plate IV). There are spirally twisted hairs among the one-celled undifferentiated hairs with smaller or larger side tubers, having longer or shorter side branches as well as hairs with different longitudinal axis, and even branching-off hairs. In the case of *Arctium lappa* also multicellular, branching-off root hairs could be observed (Picture 2, Plate IV).
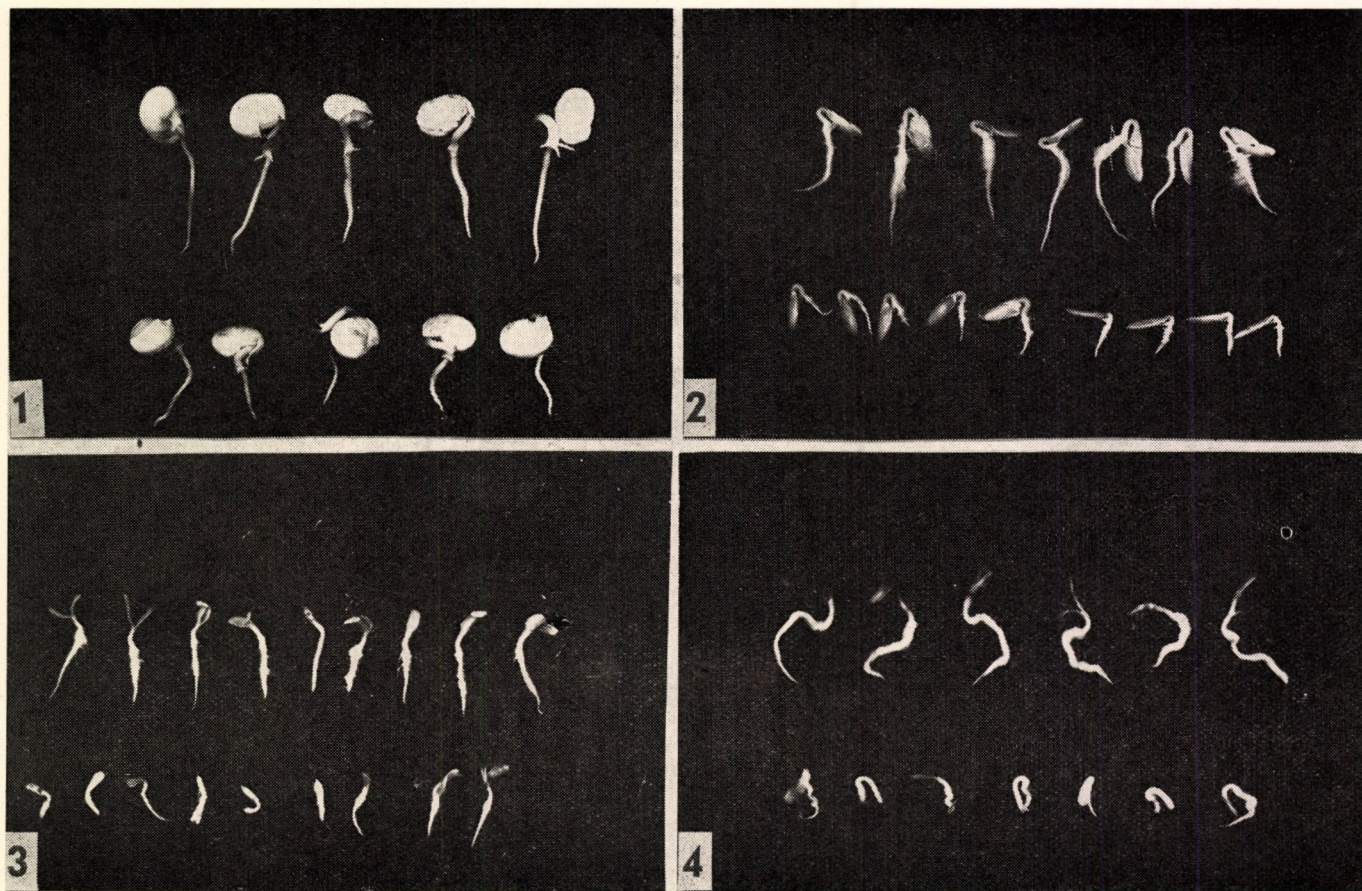
Plate I. Picture 1: 5 day control (above), and arctiine-treated (below) *Phaseolus vulgaris* seedlings. Picture 2: 5 day control (above), and arctiine-treated (below) *Cucumis sativus* seedlings. Picture 3: 3 day control (above), and arctiine-treated (below) *Lactuca* seedlings. Picture 4: 7 day control (above), and arctiine-treated (below) *Arctium lappa* seedlings

(c) *The interaction of arctiine and nucleic acids*

The results are shown in Figures 2—5. The corresponding absorption and CD spectra are given together. It is conspicuous that the absorption curves give no information about the interaction between nucleic acids and arctiine, i.e. the sums of the arctiine and the nucleic acids spectra taken separately do
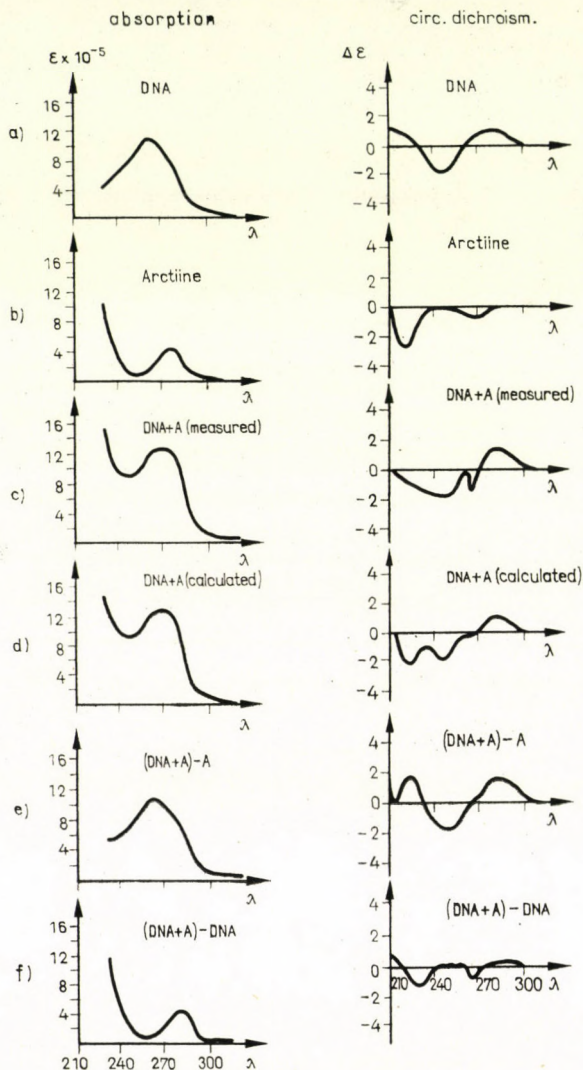
Fig. 2. Interaction between DNA and arctiine. (a) Absorption and circular dichroism of DNA. (b) Absorption and circular dichroism of arctiine. (c) Absorption and circular dichroism of DNA and arctiine together. (d) Calculated absorption and circular dichroism of DNA and arctiine. (e) (DNA + A)—A difference spectrum. (f) (DNA + A)—DNA difference spectrum
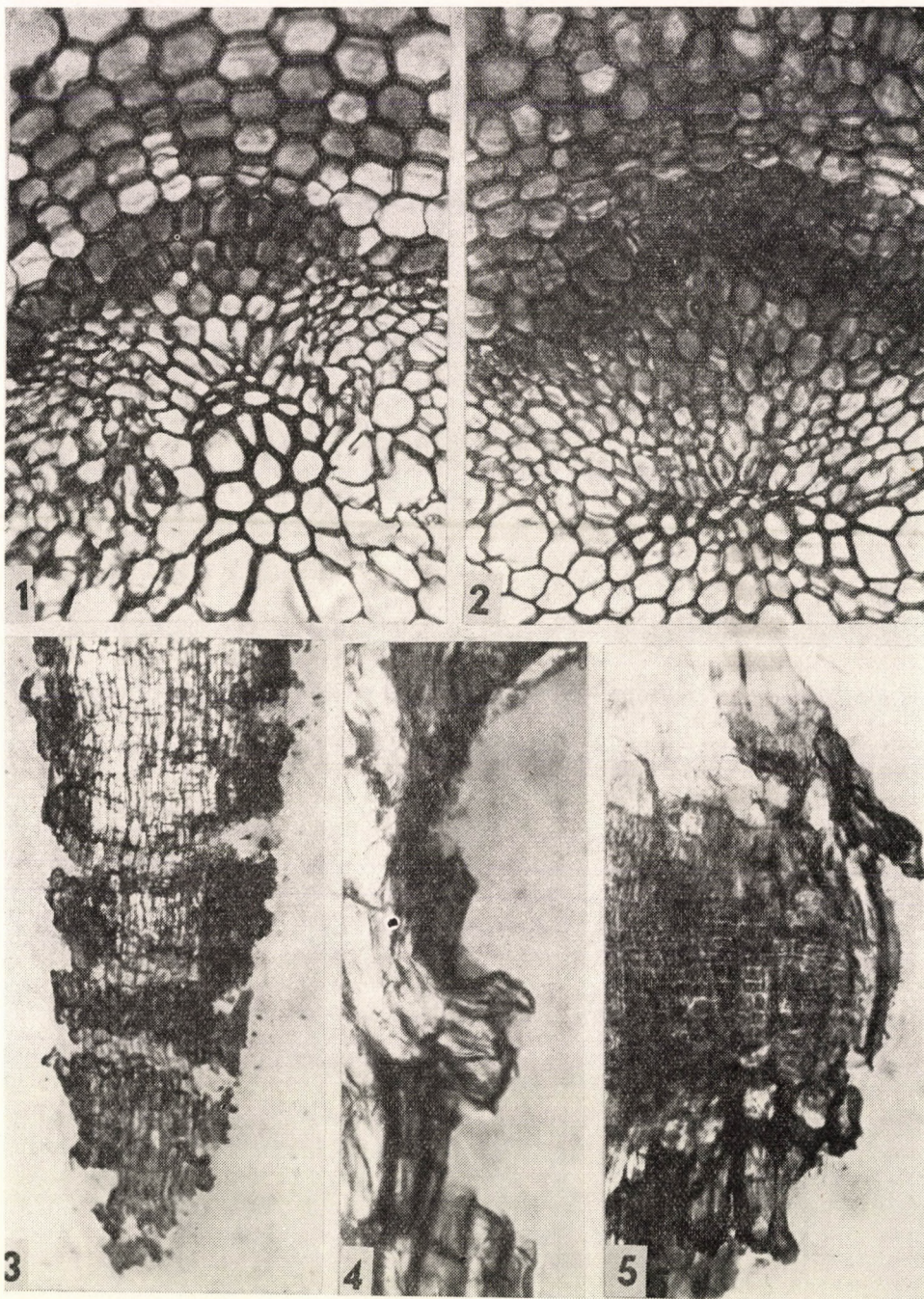
Plate II. Picture 1: Control root cross-section in *Phaseolus vulgaris* (×200). Picture 2: Root cross-section of *Phaseolus vulgaris* treated with arctiine (×200). Picture 3: Suberification and destruction in the main root of *Cucumis savitus* treated with arctiine (×80). Picture 4: Suberification of root-phloem parenchyma in *Cucumis sativus* treated with arctiine (×500). Picture 5: Suberification of radicle in *Cucumis sativus* treated with arctiine (×500)

not differ from the spectrum showing the absorption by the two compounds mixed. On the other hand, from the CD curves it is clear that arctiine and the nucleic acids have entered into some kind of interaction; the so-called sum-curves essentially differ from the spectra taken after half an hour's interaction.

It is primarily the CD band in the higher wavelength, which becomes more expressed; the plus values considerably increase. The negative CD band
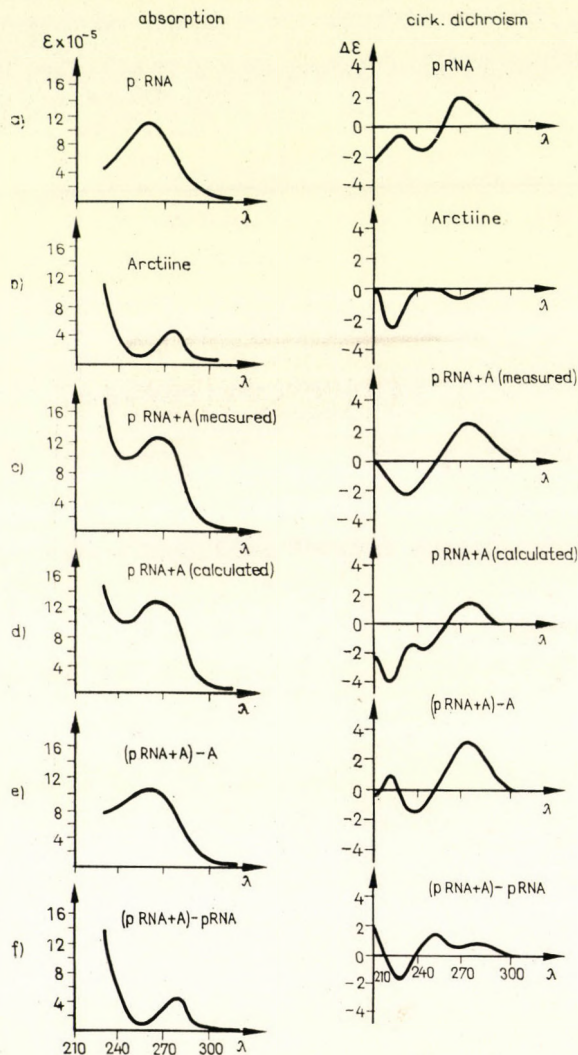
Fig. 3. Interaction between polymerized RNA and arctiine. (a) Absorption and circular dichroism of pRNA. (b) Absorption and circular dichroism of arctiine. (c) Absorption and circular dichroism of pRNA and arctiine together. (d) Calculated absorption and circular dichroism of pRNA and arctiine. (e) (pRNA+)A – A difference spectrum. (f) (pRNA+A) – pRNA difference spectrum
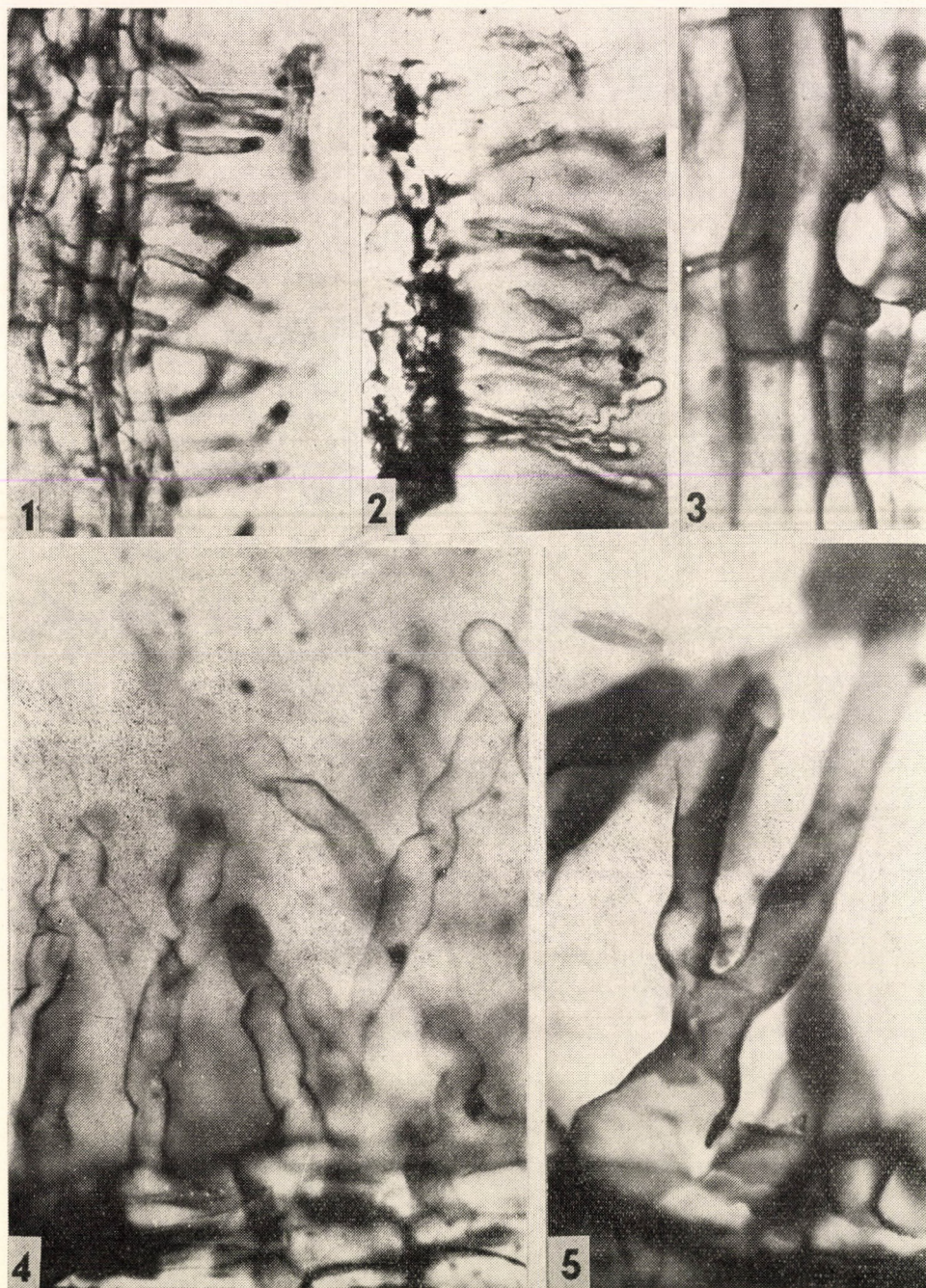
Plate III. Picture 1: Control epiblema in *Lactuca sativa* (×200). Picture 2: *Arctium lappa* epiblema treated with arctiine (×200) Picture 3: Growing rhizodermis cell in *Phaseolus vulgaris* treated with arctiine (×500). Picture 4: Root-hairs in *Phaseolus vulgaris* treated with arctiine (×500) Bifurcating. Picture 5: root hair in *Phaseolus vulgaris* treated with arctiine (×500)

in the low wavelength region does not change so definitely, but the interaction is clear on the basis of this band as well. If the differences between the so-called sum-spectra are considered (Figs 3 and 5) it will be seen that arctiine has entered most strongly into interaction with the yeast RNA and with the highly polymerized RNA. The spectrum taken from DNA and tRNA together with arctiine suggests essentially smaller changes in conformation (Figs 2 and 4).

No closer aspect of the interaction between the phenolic germination inhibitor and nucleic acids is known. Unfortunately, the CD maxima of arc-
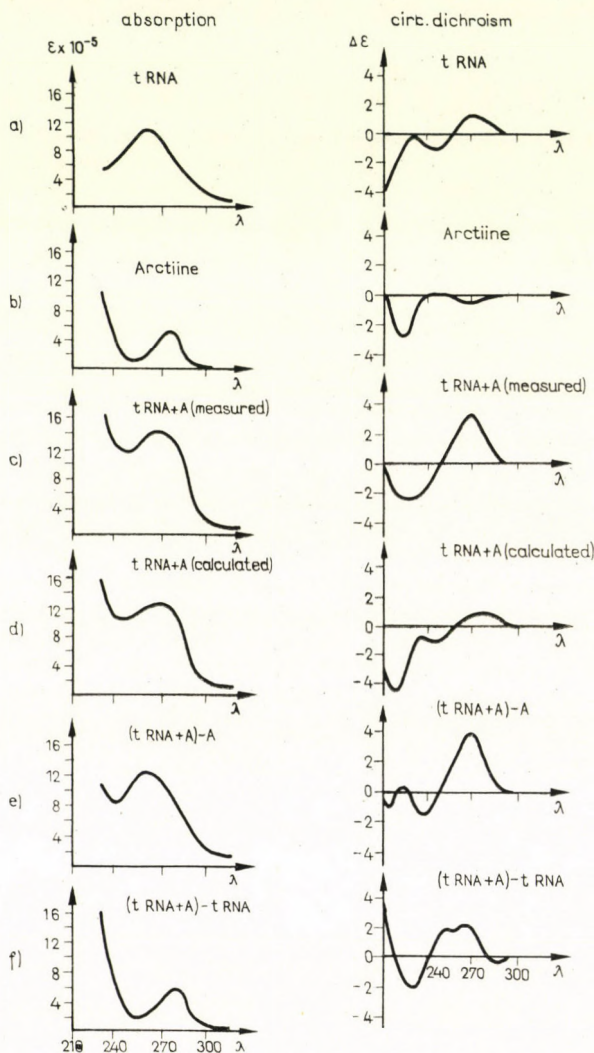
Fig. 4. Interaction between tRNA and arctiine. (a) Absorption and circular dichroism of tRNA. (b) Absorption and circular dichroism of arctiine. (c) Absorption and circular dichroism of tRNA and arctiine together. (d) Calculated absorption and circular dichroism of tRNA and arctiine. (e) (tRNA+A)−A difference spectrum. (f) (tRNA+A)−tRNA difference spectrum
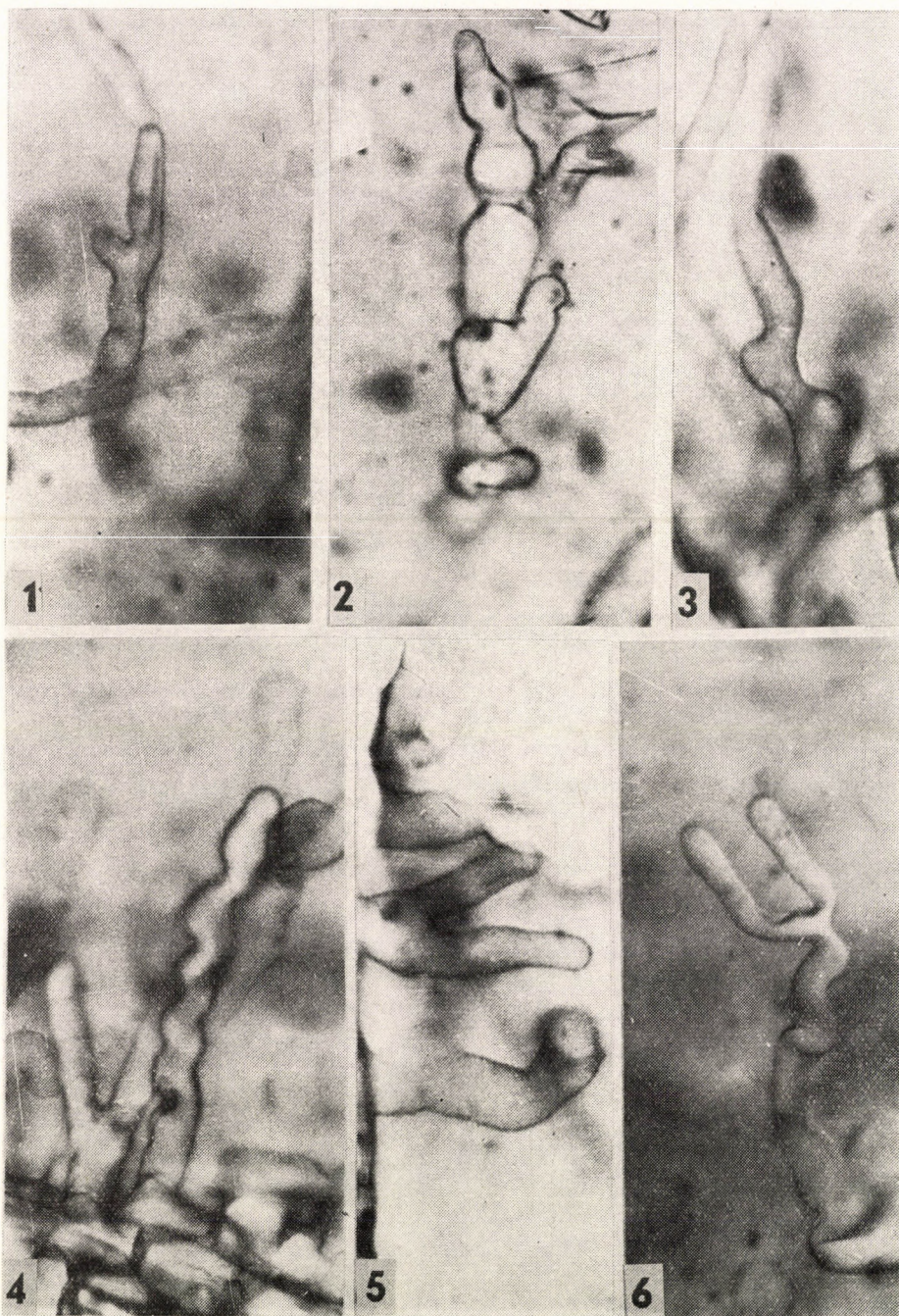
Plate IV. Picture 1: Bifurcating root-hair in *Arctium lappa* treated with arctiine (×500). Picture 2: Multi-celled, bifurcating root-hair in *Arctium lappa* treated with arctiine (×500). Picture 3: Root-hair in side-tuberred *Lactuca sativa* treated with arctiine (×500). Picture 4: Spiral and bifurcating root-hairs in *Arctium lappa* treated with arctiine (×500). Picture 5: Bifurcating and irregularly growing root-hairs in *Lactuca sativa* treated with arctiine (×500). Picture 6: Branching-off root-hairs in *Lactuca sativa* treated with arctiine (×500)

tiine and of nucleic acids are too near to each other in the system, hence it is very difficult to determine what the difference between the "joint"-spectra and the sum spectra can be attributed to. Several works are known in the literature about investigations of the interaction between nucleic acids and dyes. The absorption maximum of dyes are very far from the absorption band of DNA, so it was easy to tell to what extent the dye and the CD curve of the nucleic acid, respectively changed.
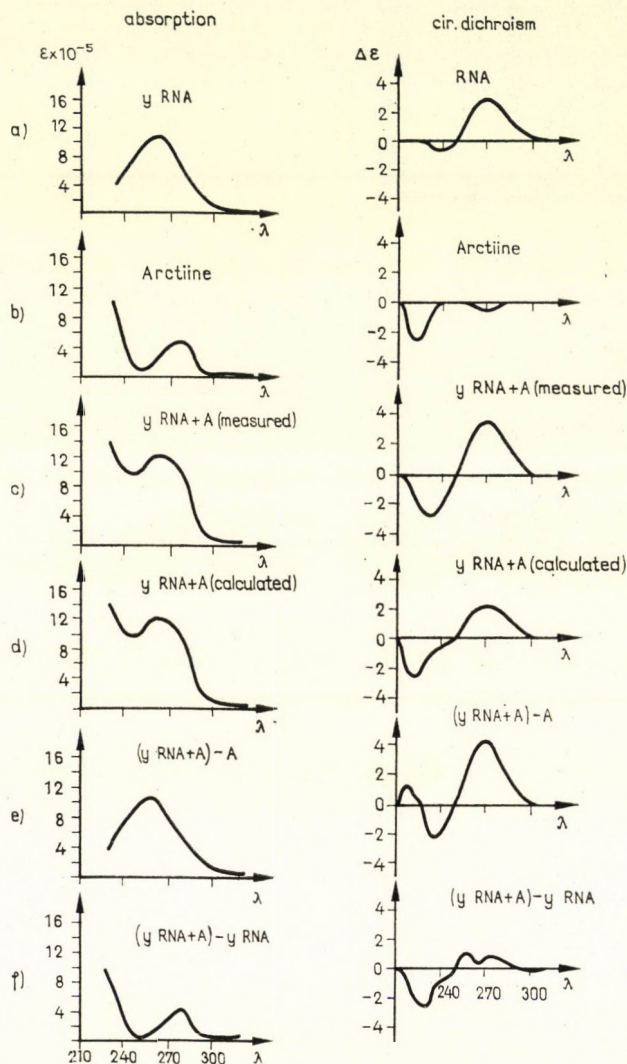
Fig. 5. Interaction between yeast RNA and arctiine· (a) Absorption and circular dichroism of yRNA. (b) Absorption and circular dichroism of arctiine. (c) Absorption and circular dichroism of yRNA and arctiine together. (d) Calculated absorption and circular dichroism by yRNA and arctiine. (e) (yRNA+A)—A difference spectrum. (f) (yRNA+A)—yRNA difference spectrum

Two kinds of interaction can in essence be distinguished: (1) Bindings occur between the anion binding sites and the anions so that the dye molecule coils itself as it were around the nucleic acid helix. (2) The dye molecule penetrates in between the bases and thus a so-called dispersion or exciton interaction may evolve. In the present case — as has been said above — it is extremely difficult to say anything definite, as the CD bands of arctiine and of the nucleic acids are very near to each other. Even so, the problem was approached in the following way.

(a) The hypothesis was that the CD spectrum of arctiine does not change substantially in the presence of nucleic acid. The spectrum of arctiine was sub-
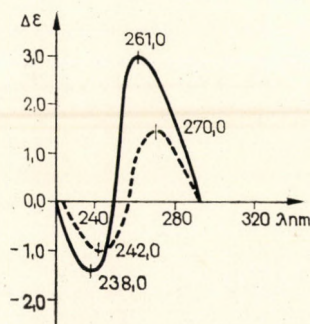
Fig. 6. Circular dichroism of RNA at 40°C and at 20°C

stracted from the "joint" spectrum. The difference spectra so obtained show the conformation change of the nucleic acid (see "e" in Figs 2—5). It must be emphasized here that the difference spectra obtained in this way are not irreal, but characteristic of nucleic acids having a higher helix content. In order to prove this, experiments were carried out. It is well known that the structure of the nucleic acid is very sensitive to temperature. At a high temperature helix conformation decreases. According to Fig. 6, the CD spectrum shows a higher maximum due to a higher conformation at 20°C than at 40°C. The spectrum of yeast RNA + arctiine is closer to the type measured at 20°C than to the spectrum observed at 40°C. In the presence of arctiine the CD spectrum changes as if the temperature had been reduced. This is valid for all nucleic acids.

(b) On the other hand, if the conformation of the nucleic acids is not supposed to change in the presence of arctiine then one has to substract from the "joint" spectrum ("f" in Figs 2—5). However, in this way a plotting will be obtained which is difficult to treat theoretically, at least according to the present state of knowledge. For, if the arctiine had coiled up round the nucleic acid helix, then both CD bands should have changed at the same rate in the

positive direction, similar to the observations of BLOUT and co-workers (1965) concerning the interaction between helix molecules and dyes. According to their experiments, dyes coiled up round the left handed helix produce a negative CD.

Shortages in data preclude a more detailed speculation. It can be inferred only that arctiine enters into interaction with nucleic acids resulting in an conformational change of the nucleic acids. The nature of the interaction is unknown. According to our knowledge this is the first case that an *in vitro* interaction between nucleic acids and growth regulating phenolic has been proved. It should be noted here that the *in vitro* interaction between gibberellic acid and nucleic acids was already demonstrated, but of a quite different type from the one observed here (KESSLER 1969).

Summary

The physiological effect of a phenol-type substance, arctiine and arctigenine, was investigated on different levels of organization.

(1) During the germination of *Arctium lappa*, the arctigenine content gradually decreases. The germination shows a endogene rhythm which is followed by the quantitative change of the arctigenine in alcohol insoluble fraction. Arctigenine is detectable in the generative organs of *Arctium lappa*. Arctigenine is not specific for one species, it can be found in the seeds of other plants within the family *Compositae* as well. According to experiments, its occurrence depends on the systematic place of the particular plant.

(2) Treatment with arctiine markedly inhibits the growth of seedlings, although it has no uniform effect on the various species. It does not influence the anatomy of the stem. Concerning the root, arctiine above all disturbs the growth of trichoblasts, it induces abnormal growth. By its effect, short bifurcating, twisted root hairs occur frequently. It has a strong destructive influence on the root of certain plants, resulting in an early suberification of the primary phloem. Presumably this causes serious disturbances in nutrient absorption.

(3) The interaction between arctiine and the nucleic acids of different origin shows that arctiine changes the structure and increases the double helix (?) conformation of the nucleic acids. The nature of the interaction is not known and it cannot be brought into relation with the germination regulating effect of arctiine or arctigenine.

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REGULATION OF THE GROWTH OF TOBACCO TISSUES WITH CYTOKININ AND AUXINS

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The growth regulation of isolated tobacco tissues (*Nicotiana tabacum* L.) was examined in the function of various concentrations and concentration combinations of auxins (indoleacetic acid, IAA; dichloro-phenoxy-acetic acid, 2,4-D) and of benzimidazole (BIA). The aim of the experiments was to obtain data on the effect of compounds applied on the tissue growth, and on their effect mechanism as well as to support the cytokinin-like effect of benzimidazole. From the results it can be inferred that IAA and BIA as a function of concentration stimulate tissue growth, while 2,4-D as a function of concentrations applied showed maximum curve. On applying IAA and 2,4-D together, antagonism prevails, since IAA reduces the stimulation by 2,4-D, most effective in tissue growth, while the inhibition by 2,4-D alone cannot be counterbalanced even by the most effective IAA concentration. Tissue growth and increase in protein content in the case of IAA are parallel, while in the case of 2,4-D protein content rises at the concentration inhibiting tissue growth, so here the inhibition of tissue growth prevails not through the inhibition of protein synthesis. Cell numbers calculated for the unit of weight increase in general with concentrations, so the weight of the individual cells lessens. BIA applied together with IAA shows an additive effect, while 2,4-D with this effect is not general. BIA, although it is not a purine-structured compound, has an effect in tissue growth similar to that of "real" cytokinins.

Introduction

Hormonal regulation of growth and of differentiation is one of the focal questions of the plant physiological research today. The examination of phytohormones has resulted in considerable development not only in theory but also in the practice of several decades. In spite of this fact, the mechanism effect of growth-regulating materials, the hormonal regulation of plant differentiation is not clarified even today (OVERBEEK, 1968, PILET, 1961, STREET, 1966, 1969).

The number of compounds demonstrably possessing hormonal activity is ever more increasing. Many data exist with reference to the fact that compounds with hormonal effect, even though they may belong in the same group, produce their effect not in the same way (LINSMAIER and SKOOG, 1965, MARÓTI, 1970, SHANTZ, 1966, STEWARD et al., 1969, STEWARD and SHANTZ, 1956).

These were the problems that provoked the examination of three compounds of hormonal character with respect to their effect on the growth of tobacco callus tissue and on their protein and nucleic acid metabolism. The three compounds are as follows: a natural auxin: β-indoleacetic acid (IAA);

a synthetic auxin: 2,4-dichlorophenoxy-acetic acid (2,4-D); and a synthetic material of cytokinin activity: benzimidazole (BIA) (SZIRÁKI, 1970).

In the experiments the effect of the two auxins separately, the interactions of the two compounds, and in suitable concentration combinations have been examined. On the other hand the cytokinin activity of BIA at various concentrations, as well as in applying it together with IAA and with 2,4-D, was also examined. The experiments with benzimidazole are of interest because BIA — although it is not a purine structured compound — has already showed cytokinin activity in several biological tests (POZSÁR et al., 1967, KIRÁLY, 1968, KING and HSU, 1963, MISHRA and WAYGOOD, 1964, WANG et al., 1961).

Material and method

Callus tissue isolated from the stem of *Nicotiana tabacum* L., and stored in culture for years was used as test material in the examinations. Under experimental conditions the tissue consisted of loose, yellowish-greenish cell mass of intensive growth. The tissue did not show either tissue differentiation or inherent organization in the culture medium used for its sustenance. The basic culture medium used for the experiment was the slightly modified variation of "Z" culture medium described by MARÓTI (1969). To the basic culture medium the following concentrations of the examined materials with a hormonal effect were given: 0.8—4.0—20.0 mg/l IAA; 1.2—6.0—30.0 mg/l 2,4-D and 4.0—20.0—100.0 mg/l BIA.

During the inoculation carried out in sterile conditions, 200 mg of inoculum was placed in the culture medium in 100 ml ERLENMEYER-type flasks. Incubation time was 3 weeks. The cultures were stored at ambient temperature and in light-dark conditions as prevailing in nature. The growth and metabolism reactions of callus tissues were determined from measurements of fresh and dry weights, changes in cell numbers, and from total nucleic acid and protein content. Counting of cell numbers was carried out with the aid of a BÜRKER chamber (BROWN and RICKLESS 1950).

The extraction necessary for the determination of the nucleic acid (NA) content was carried out with a modification of the OGUR—ROSEN procedure (OGUR and ROSEN 1950). From the optical density value measured at 260 nm, and with consideration to dilution and hyperchrom effect, the quantity of nucleic acid in mg; for 1 gr fresh weight can be calculated. The material put aside at the end of removing the nucleic acid was used for determination of protein (Pr; LOWRY et al. 1951).

When the extinction measured at 680 nm and the dilution was known the protein content for 1 gr fresh weight could be established by means of a protein concentration range.

The experimental value data have been calculated from the average ($\bar{X}$) of four parallel experiments, i.e. of some 20 flasks; along with the values also the standard error of measurements (s) are indicated (SNEDECOR 1956). The daily growth is obtained as the quotient of the differences between the end and initial weights of the tissues and of the incubation period (day), while the relative growth is the quotient of the end and initial weight differences and of the initial growth (MARÓTI 1969).

Results

The values of end weight, daily growth, relative growth and cell number obtained during the first experiment series are given in Table 1. Here IAA and 2,4-D as well as their various concentration combinations were given to the nutrient media. Considering the effect of the various 2,4-D concentrations given to the IAA concentration concerned, it can in general be inferred that — in comparison with the control (IAA=O, 2,4-D=O) — among the applied three differing 2,4-D concentrations at the concentration of 1,2 mg/l a stronger

Table 1

Effect of IAA and 2,4-D concentrations on the tissue growth of tobacco

($\bar{X}$ = average, s = standard error)

IAA mg/l	Metabolism indices	2,4-D mg/l							
		0.0		1.2		6.0		30.0	
		$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s	$\bar{X}$	s
0.0	End weight, mg	302.1	31.3	819.2	84.6	675.5	52.4	200.5	24.6
	Dry weight, %	8.3	1.2	7.7	0.3	7.3	0.3	8.0	0.6
	Cell number, 10^5/g	15.6	4.4	17.9	3.9	17.4	5.2	25.2	6.1
	Daily growth	4.9	—	29.5	—	22.6	—	0.02	—
	Relative growth	0.5	—	3.1	—	2.4	—	0.04	—
0.8	End weight, mg	423.0	46.3	410.2	69.1	362.8	52.9	171.5	9.4
	Dry weight, %	7.5	0.7	7.0	0,7	7.0	0.7	7.9	0.6
	Cell number, 10^5/g	12.5	4.7	19.3	4.1	18.0	6.9	19.2	3.4
	Daily growth	10.6	—	10.0	—	7.8	—		—
	Relative growth	1.1	—	1.1	—	0.8	—		—
4.0	End weight, mg	514.9	64.2	470.5	63.1	343.1	44.3	168.3	10.3
	Dry weight, %	6.7	0.7	7.7	0.4	7.4	0.3	6.3	0.6
	Cell number, 10^5/g	18.9	5.2	16.6	7.9	14.5	4.6	17.4	6.7
	Daily growth	14.9	—	12.8	—	6.8	—		—
	Relative growth	1.6	—	1.4	—	0.7	—		—
20.0	End weight, mg	605.0	43.4	659.7	37.5	465.5	53.2	170.6	13.5
	Dry weight, %	7.5	0.7	7.4	0.4	7.2	0.4	6.8	0.6
	Cell number, 10^5/g	24.5	3.2	31.3	6.7	31.9	6.2	14.0	3.5
	Daily growth	19.3	—	21.9	—	12.6	—		—
	Relative growth	2.0	—	2.3	—	1.3	—		—

growth while at 6.0 mg/l a weaker growth manifests itself; 2,4-D applied in the 30.0 mg/l concentration caused full inhibition in all cases during the growth of the callus; 2,4-D applied alone at 1.2 mg/l concentration, results in a 170 per cent weight increase in comparison with the control. The IAA concentrations alone showed a reversed growth tendency as the 2,4-D. Here the weaker growth stimulation appeared in the lowest (0.8 mg/l) concentration while the stronger growth stim ulation in the highest (20 mg/l) concentration. The absolute data of tissue growth correlated with the daily and the relative growth values, which confirm the above conclusions.

When examining the effect of the various concentration combinations of 2,4-D and IAA, it can be observed that the growth stimulating effect of the two auxins does not add up, furthermore, that even the combination of IAA

Table 2

Effect of IAA and BIA concentrations on the growth of tobacco tissue
($\overline{X}$ = average, s = standard error)

IAA mg/l	Metabolism indices	BIA mg/l							
		0.0		4.0		20.0		100.0	
		$\overline{X}$	s	$\overline{X}$	s	$\overline{X}$	s	$\overline{X}$	s
0.0	End weight, mg	472.8	85.8	419.4	60.7	500.9	63.2	634.1	56.4
	Dry weight, %	6.6	0.7	7.5	0.9	7.4	0.6	7.2	0.5
	Cell number, 10^5/g	12.9	3.4	11.1	1.5	17.8	4.1	19.1	3.9
	Daily growth	13.0	—	10.5	—	14.3	—	20.7	—
	Relative growth	1.4	—	1.1	—	1.5	—	2.2	—
0.8	End weight, mg	593.4	80.0	585.7	45.7	607.0	70.1	511.6	81.1
	Dry weight, %	7.9	0.7	7.1	0.8	7.6	0.4	8.0	0.3
	Cell number, 10^5/g	15.2	4.3	14.1	3.3	16.0	3.3	24.9	5.2
	Daily growth	18.7	—	18.3	—	19.4	—	14.8	—
	Relative growth	2.0	—	1.9	—	2.1	—	1.5	—
4.0	End weight, mg	633.4	47.4	904.3	90.9	820.2	88.6	377.6	49.8
	Dry weight, %	6.6	0.6	5.3	0.5	6.6	0.6	7.9	0.7
	Cell number, 10^5/g	18.4	5.2	10.2	1.4	14.2	3.1	21.8	2.0
	Daily growth	20.6	—	33.5	—	29.5	—	8.5	—
	Relative growth	2.1	—	3.5	—	3.1	—	0.9	—
20.0	End weight, mg	734.6	63.5	931.5	53.7	947.8	82.4	621.0	59.7
	Dry weight, %	6.6	0.6	6.1	0.5	5.8	0.5	6.8	0.7
	Cell number, 10^5/g	25.9	6.2	13.1	3.2	18.9	3.5	23.8	3.9
	Daily growth	25.5	—	34.8	—	35.6	—	20.5	—
	Relative growth	2.7	—	3.6	—	3.7	—	2.1	—

of an optimal concentration with 2,4-D of the most effective concentration does not result in such a growth stimulation as when applying 2,4-D alone in 1.2 mg/l concentration.

The percentage ratio of the dry weight — in comparison with the control (8.3 per cent) — varies between 8.6—6.3 per cent.

The cell-number calculated for the unit fresh weight of both the individual compounds and the variations treated with the combinations of these is in general of the same order as that of the control. With the increase of the concentration of the applied compounds, however, the cell numbers increase within the order, they may be even twice as many as those in the control. This in essence means that the number of cells within the same unit weight will be more, therefore the weight of the individual cells decreases.

Table 3

Effect of 2,4-D and BIA concentrations on the growth of tobacco tissue

(X = average, s = standard error)

2,4-D mg/l	Metabolism indices	BIA mg/l							
		0.0		4.0		20.0		100.0	
		$\overline{X}$	s	$\overline{X}$	s	$\overline{X}$	s	$\overline{X}$	s
0.0	End weight, mg	584.9	59.6	897.7	79.1	958.0	81.3	1108.2	102.3
	Dry weight, %	7.5	0.6	7.0	0.5	6.8	0.9	6.8	0.6
	Cell number, 10^5/g	10.5	1.4	8.9	2.8	9.0	3.3	9.1	2.2
	Daily growth	18.3	—	33.2	—	31.1	—	43.7	—
	Relative growth	1.9	—	3.5	—	3.8	—	4.5	—
1.2	End weight, mg	744.4	71.7	816.4	73.5	1045.5	55.9	911.8	74.6
	Dry weight, %	5.9	0.7	5.7	0.3	5.8	0.4	6.5	0.4
	Cell number, 10^5/g	13.7	3.3	12.7	1.5	9.5	2.8	15.4	3.2
	Daily growth	25.8	—	29.4	—	40.3	—	33.9	—
	Relative growth	2.7	—	3.1	—	4.2	—	3.6	—
6.0	End weight, mg	546.7	46.2	668.9	49.7	672.7	38.8	520.9	60.9
	Dry weight, %	6.1	0.5	5.3	0.4	6.0	0.4	6.8	0.4
	Cell number, 10^5/g	17.9	5.3	15.1	4.4	11.2	1.5	17.1	4.1
	Daily growth	16.5	—	22.3	—	22.5	—	15.3	—
	Relative growth	1.7	—	2.3	—	2.4	—	1.6	—
30.0	End weight, mg	209.6	26.9	208.2	38.9	193.2	27.5	212.8	18.1
	Dry weight, %	6.6	0.7	6.9	0.9	6.8	0.4	6.9	0.5
	Cell number, 10^5/g	25.3	5.6	34.1	6.5	24.4	3.2	15.6	3.6
	Daily growth	0.5	—	0.4	—		—	0.6	—
	Relative growth	0.05	—	0.04	—		—	0.06	—

In the second series of experiment the effect of IAA and BIA concentrations was examined. The values are given in Table 2. Under the effect of IAA treatment the tissue growth trend is the very same as in the preceding experiments; with the increase in the concentration, the growth intensity also rises. However, the absolute and the correlated values indicating the tissue growth are somewhat greater, which is explainable by the temperature differences during the experiments, with the different times of light and darkness, and with the differing weight of tissue inocula. Increasing BIA concentrations alone result in not a considerable but in a definite growth. In the combinations of the two compounds this weight-increasing tendency can also be noticed, whereas in higher concentration combinations, especially in 100 mg/l BIA, some growth inhibition can also be observed.
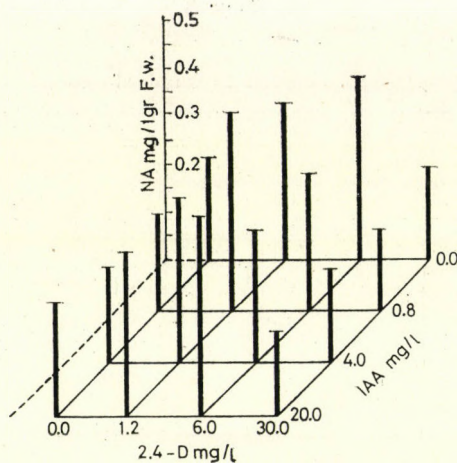
Fig. 1. Effect of IAA and 2,4-D concentration combinations on the NA content of the tobacco callus tissue (F. w. = fresh weight)
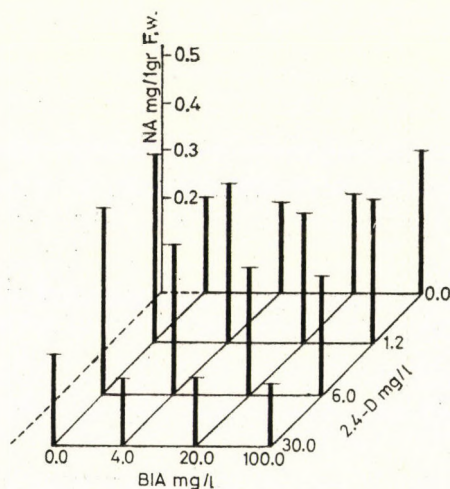
Fig. 2. Effect of 2,4-D and BIA concentration combinations on the NA content of the tobacco callus tissue (F. w. = fresh weight)

The dry weight percentage of the tissues is identical with the data found in the preceding experiments. The cell number found in the unit weight here also increases, in general in both compounds, with the increase of the concentrations. Essentially the same can be observed in the combinations.

The effects of 2,4-D and of BIA concentrations are shown in Table 3. As regards the growth of tobacco tissue 2,4-D alone shows an effect strongly dependent on concentration, and the weight increase is ever more inhibited

with the increase in concentration. This phenomenon was observed also in the first series of experiments. On the other hand, with the increase of concentration BIA promotes weight increase also here — similarly as was the case in the second series of experiments — although the absolute values are not identical. In the combinations of the two compounds mainly the effect of 2,4-D seems to prevail, since with the increase in its concentration (6 → 30 mg/l) the weight increase is ever more and eventually completely inhibited; the sti-
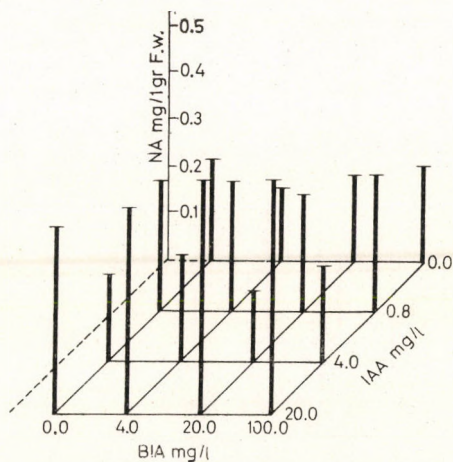
Fig. 3. Effect of IAA and BIA concentration combinations on the NA content of the tobacco callus tissue (F. w. = fresh weight)
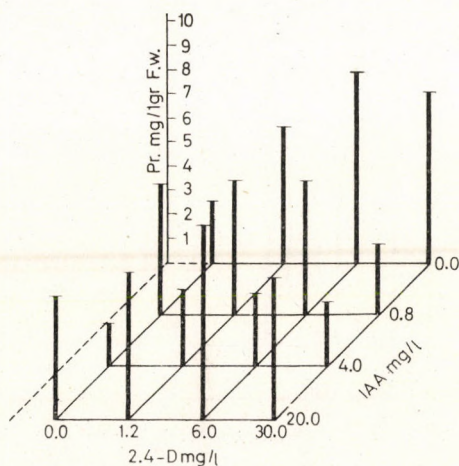
Fig. 4. Effect of IAA and 2,4-D concentration combinations on the Pr content of the tobacco callus tissue (F. w. = fresh weight)

mulating effect of BIA does not appear at all. This effect is fairly well reflected also by the rest of the metabolism indices calculated. Under the effect of the 2,4-D and BIA concentration combinations, the dry weight content of the fresh weight varied between 5.3—7.5, which is hardly differing from the values obtained in the other two series.

The changes in the nucleic acid and protein contents of the tissues are given in Figures 1—6 in mg per unit weight (gr). The nucleic acid data correlated for 1 gr fresh weight showed values of 10^{-1} mg order, both in the controls and in the individual variants. The values of the protein content were one order higher throughout.

Under the effect of the applied 2,4-D concentration the NA change show a maximum-curve, in which the highest concentration (30 mg/l) indicates synthesis inhibition in comparison with the control (Fig. 1). This trend appears in the fresh weight data as well. Under the effect of the IAA concentration, NA shows values similar to the control values or higher than those, but it changes not proportionately with the increase in concentrations (Figs 2, 3).

This change does not manifest itself in the alterations of weight and of cell number. Although under the effect of the concetration combinations of the two compounds, the absolute values of NA synthesis change, but the same tendencies prevail as noticeable when the compounds are applied alone. With the increase in BIA concentration, the NA content of the unit weight also increases. In its combinations with IAA, the NA content of the fresh weight is still considerably increasing, while in its combinations 2,4-D it decreases.
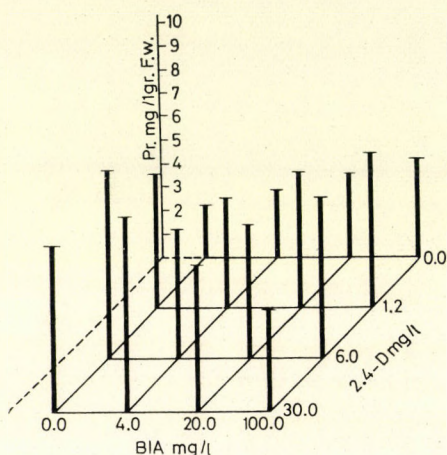
Fig. 5. Effect of 2,4-D and BIA concentration combinations on the Pr content of the tobacco callus tissue (F. w. = fresh weight)
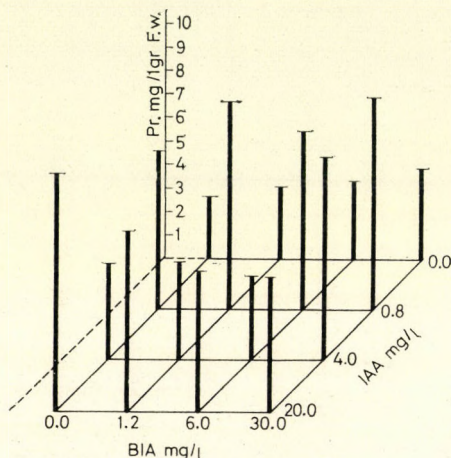
Fig. 6. Effect of IAA and BIA concentration combinations on the Pr content of the tobacco callus tissue (F. w. = fresh weight)

In the former case the effect of the two compounds is somewhat adding up, while in the latter case some antagonism is evoked. This change in NA is well observable — especially in the combination with 2,4-D — also in the tissue growth.

The protein content in the control tissues is in general 10—20times higher than the NA content (Figs 4—6). IAA concentrations alone raise this rate 21—29times by themselves. In applying 2,4-D alone, the difference is 14—37times greater, while in BIA it is 14—19times greater, i.e. so many times more mg Pr than NA can be found in one gr fresh tissue. The ratio of the two examined metabolism indices in general remains within the same limits under the effect of concentration combinations of the individual compounds, too.

Discussion and conclusion

By our experiments we wanted to obtain data on the growth-regulating mechanism of known phytohormones (IAA, 2,4-D) on the one hand, and intended to trace the cytokinin activity of BIA on the other. Naturally, the com-

bined application of the compounds used made it possible to acquire knowledge on both their synchronous and antagonistic effects. This later question is important because ever more data testify that growth regulation is in general a consequence of not one biologically active substance (phytohormone, cytokinin, vitamin, etc.), but the result of an appropriate proportion of several compounds of such character (LINSMAIER and SKOOG 1965, MARÓTI 1970, MURASHIGE and SKOOG 1962, STEWARD et al. 1969).

Before evaluating the results of the experiments the question may arise whether the compounds applied within such wide concentration limits can give satisfactory information concerning the mechanism of their effect. When setting the experiments our aim was to obtain with them — as preliminary experiments — a general orientation on our test material. These results may accurately determine the concentrations for our later experiments. On the other hand, similar concentrations were also applied by other authors, who launched their investigations with similar aims; e.g. within similar or even wider limits, CAREW and STABA (1965) examined the effect of 2,4-D; HILDEBRANDT (1962) that of 2,4-D and IAA; MURASHIGE and SKOOG (1965) that of IAA; KIRÁLY (1968), POZSÁR et al. (1967) that of BIA.

The deviating weight increase and metabolism indices of the materials applied alone did not always agree with those in the various series, resp. controls. This fact may raise objections when evaluating the results. In connection with this, it should be taken into consideration that the experiments took a long time during which neither temperature nor light conditions could be uniformly regulated. Besides, a slight although weighed difference occurred also in the initial weights of the tissues. All these suffice to cause differences in the intensity of tissue growth in experiments of such a short incubation time, as is also known from the data of the literature (CAPLIN 1963, GAUTHERET 1959, HILDEBRANDT 1962, MARÓTI 1969). The results of the individual experiments provide therefore satisfactory basis only for comparisons within one series. For the establishment of the tendency in metabolism changes, however, the results of the various series are also suitable.

By comparing the results of the experiments, it can be inferred that the effect of IAA and 2,4-D dosed together is not additive in tissue growth. Furthermore, suboptimal IAA concentrations reduce the stimulating effect of optimal 2,4-D concentration. At the same time, the inhibitory effect of 2,4-D applied in high concentration cannot be counteracted by even the most effective IAA concentration, so in the effect of the two compounds a certain antagonism prevails. According to several researchers (FANG and TE CHANG YU 1965, OKAZAWA et al. 1967) the mechanisms of IAA and of 2,4-D are different. This is supported also by our results. While the highest growth rate and protein content associate with the highest IAA concentration, in the highest 2,4-D concentration — where absolute growth inhibition is observed —

the protein content is higher than that in the concentrations causing the most intensive growth. From this it follows that 2,4-D produces its growth inhibiting effect not by inhibiting the protein synthesis. According to FANG and TE CHANG YU (1965), low 2,4-D concentrations stimulate, its high concentrations inhibit, the respiration of plant tissues. Presumably, the growth inhibiting effect of 2,4-D can be attributed to this fact in our experiments too.

At present, researchers hold various views on the primary effect mechanism of auxins. Some of them regard auxin as the initiator of the polypeptid chain (ARMSTRONG 1966), while others interpret it as the RNase regulator (TRUELSEN 1967). According to SACHER (1967), also auxins exert their primary influence upon RNA and it is through this that they act on protein synthesis. SUIGURA et al. (1962) observed that in tobacco leaves the protein level changed parallel with the change in the nucleic acid level, a consequence of the effect of kinetin. This is supported by our results to the extent that the change in the nucleid acid level is followed by a change in protein level, of identical sign but not of an identical rate, if the auxins applied are dosed alone. When the two auxins are simultaneously dosed into the culture medium, the former tendency does not definitely appear, but under the effect of the various 2,4-D concentrations with an individually fixed IAA, the change in nucleic acid level is followed by the change in protein level.

Cell number values correlated for unit weight agree with those in the literature (MARÓTI 1968, 1960). In applying IAA we could state that increasing weight values associate with increasing cell number values. This allows the conclusion that IAA dosed alone exerts its growth stimulating effect — apparently operating along with the endogenous cytokinins — by stimulating the cell division. Thus, by raising the concentration, cell weight is decreased to a certain extent. In applying 2,4-D, this phenomenon can also be observed; however, while in IAA this cell number increase is proportionate with the full weight increase, in 2,4-D we counted most cells, in the most inhibited tissue weight category, therefore those with the smallest weight. In the course of a combined application of IAA and 2,4-D in certain concentration combinations, some synergism prevails as to the changes in cell number.

In general, BIA stimulates tissue growth as a function of concentration. From the cell number data it can be inferred that here the weight increase is a consequence partly of cell division, partly of cell growth. BIA and IAA dosed together in certain concentration combinations resulted in greater weight increase than the growth measured at the optimal concentration of the two hormones. It follows that the growth stimulatory effect of these two compounds is — in certain combinations — of an additive character. BIA with 2,4-D showed an additive effect only in one combination, while none of the BIA concentrations could compensate the inhibitory effect of a high 2,4-D concentration.

In benzimidazole there is C instead of 1- and 3-positioned N, characteristic of purines, so there is only space structural similarity between benzimidazole and the purine-structured cytokinins. In spite of this, several researchers observed cytokinin activity during investigations with BIA (KIRÁLY 1968, KING and HSU 1963, MISHRA and WAYGOOD 1964, POZSÁR et al. 1967, WANG et al. 1961). They inferred the cytokinin-like activity of BIA mainly from the fact that it inhibits senescence, and that its stimulating effect on protein and nucleic acid synthesis could be verified. We also directly succeeded in proving the cytokinin character of benzimidazole, because BIA had a favourable effect under the applied conditions, on both the weight increase and protein and nucleic acid synthesis of tobacco callus tissues.

Some general conclusions can also be drawn from the experiments. The results confirm the assumption that the compounds exhibiting growth activity when applied alone reinforce each other's effect when applied together, but they may also destroy it, i.e. they exhibit synergism but antagonism as well. This also proves that the growth of plant cells and tissues is in general produced not by individual compounds, but by the various, biologically active substances (auxins, cytokinins, vitamins, etc.) in harmonic proportion. — It is also apparent from the experiments that the external phenomena of tissue growth, observable also morphologically, are always preceded by the changes in nucleic acids and protein content, and that the growth stimulators effect tissue growth through these. — The cytokinin-like effect of benzimidazole was also established in our experiments, confirming some earlier statements of several authors.

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KRITISCHE REVISION DER ARUM-ARTEN DES KARPATENBECKENS

von

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The author starts from his preceding work (1971), in which he examined the infraspecific taxa of *Arum maculatum* L. and the distribution of the species, with morphological, cytological and phenological methods. He extended his investigations to other regions of the Carpathian Basin, too.

In Hungary, *Arum maculatum* occurs in the south-western half of the Transdanubia. *Arum alpinum* SCHOTT et KOTSCHY is found also in almost the whole area of Hungary, in Czechoslovakia, Romania, Yugoslavia and Austria. *Arum alpinum* SCHOTT et KOTSCHY has been considered partly *A. maculatum*, partly *A. orientale*. The leaves of *A. alpinum* are not spotted, its rhyzome is flatly, oval, obliquely ascendent, the spatha greenish; its root peduncle as long as the leaf petiole; its chromosome number 2n = 28.

The author reviews also the other European taxa (*A. italicum*, *A. Besserianum*, *A. orientale*, *A. elongatum*).

Einleitung

Schon seit KITAIBELS Forschungen weiss man, dass sich eine ganze Reihe von Pflanzentaxa bzw. »Populationen« der Karpatenländer in das System von LINNÉ — sowohl taxonomisch als auch der Nomenklatur nach — nicht recht einfügen lässt. Allerdings ist auch die Vereinigung der pannonischen, balkanischen, östlichen usw. Elemente mit den Linneonen nicht ohne Einfluss auf letztere geblieben. Die LINNÉschen Arten wurden immer heterogener, ihr infraspezifisches System immer komplizierter, was schliesslich dazu führte, dass in den verschiedenen nationalen Florenwerken — unter der gleichen Artbenennung — der Lokalflora entsprechend ganz unterschiedliche Artbeschreibungen vorkommen. Dies geschah u. a. auch im Falle der *Arum*-Populationen des Karpatenbeckens.

So wurde der ganze *Arum*-Genus-Bestand auf diesem grossen Gebiet »offiziell« für *Arum maculatum* im Sinne von LINNÉ angesehen (z. B. HEGI, 1908—1931, II. p. 133; JÁVORKA, 1925: 150—151; DOSTÁL, 1950: 2124—25; SOÓ—JÁVORKA, 1951: 974; ASCHERSON—GRAEBNER, 1904: 378). Die bedeutendsten *Arum*-Monographen (HRUBY, 1912; ENGLER, 1920) der »Neuzeit« waren der gleichen Meinung.

Im Laufe des letzten Jahrzents befassen sich wieder mehrere Autoren mit der infraspezifischen Taxonomie von *Arum maculatum* L. Für die tatsächliche Polymorphie dieser Pflanze machen die Verfasser in ihrer Mehrzahl

(MELZER apud JANCHEN, 1960: 877; BORHIDI—PRISZTER, 1967: 160—163; teilweise auch PRIME, 1961 und RIEDL, 1967) *Arum italicum* MILL. »verantwortlich«. Andere hingegen (z. B. DIHORU, 1970: 71—84) untersuchen die Verbreitung einer osteuropäischen oder (TERPÓ, 1971) einer pannonischen *Arum*-Spezies in diesem Gebiet wobei dargelegt wird, dass diese ausserordentlich krasse Heterogenität der Einordnung des betreffenden Taxons in den Formenkreis von *Arum maculatum* zuzuschreiben sei. Wieder andere — wie etwa RIEDL (l. c.) — schlagen vor, die Taxonomie »*maculatum*« durch Herauslösung eines höheren, immerhin aber noch zum *Arum maculatum* gehörenden infraspezifischen pannonischen Taxons zu ordnen.

Material und Methode

Zu den taxonomischen Untersuchungen wurden herangezogen: in Ungarn die Herbarien des Ungarischen Nationalmuseums (**Növénytár**) (**N. H.**), des Botanischen Gartens der EÖTVÖS LORÁND-Universität (**U. H.**), der Universität für Gartenbau (**KE. H**), der Zentralen Staatlichen Saatgutinspektion (**OV. H.**) — sämtliche in Budapest — sowie das Herbarium der KOSSUTH LAJOS-Universität zu Debrecen (**D. H.**); ausserhalb Ungarns: aus der DDR das HAUSSKNECHT-Herbarium der Universität Jena (**HAU. H.**); aus Polen die Herbarien der Krakauer Jagello-Universität (**J. H.**), der Warschauer Universität (**U. W.**) und der Universität in Wrocław (**WRO.**) Mein Material eigener Sammlung stammt aus Ungarn, aus der DDR und aus Jugoslawien (ein großer Teil davon ist später leider verbrannt). In der Tschechoslowakei konnte ich im Institut der ČSAV (Tschechoslow. Ak. d. Wiss.) in der Pruhonice unter Mitwirkung von Frau A. CHRTKOVÁ das **Arum**-Material dieses Instituts aufarbeiten (**PRU. H.**).
An dieser Stelle sei es mir gestattet, allen Professoren, Direktoren und Mitarbeitern der verschiedenen Lehrstühle, Institute und Herbarien für ihre freundliche und wertvolle Hilfe meinen aufrichtigen Dank auszusprechen.

Von den ausländischen Kollegen möchte ich zu allererst den Herren Prof. Dr. H. SCHINDLER, Ing. F. WEBER und Doz. Dr. H. RIEDL (alle in Wien) für die grossformatigen Photokopien der Aquarelle »Icones Aroidearum 1857« sowie für die schriftlichen Beiträge danken. Besonderer Dank gebührt Herrn Dr. S. M. WALTERS (Cambridge Univ. H.) für die Grossphotokopien von **A. maculatum** Linné, Herrn Doz. Dr. V. SKALICKY (K.-Universität Prag) und den Kollegen Dr. H. DIETRICH (Jena) und N. JANJIĆ (Sarajevo) für die regelmässige Zusendung von Literatur bzw. für ihre bei den Exkursionen und beim Sammeln geleistete tatkräftige Hilfe. Und nicht zuletzt seien meine ungarischen Kollegen genannt, denen ich Dank zolle: so vor allem für die Unterstützung durch Konsultationen und Bereitstellung von Literatur Herrn Prof. Dr. R. SOÓ, Mitglied der Ungarischen Akademie der Wissenschaften, den Herrn Prof. Dr. Z. KÁRPÁTI (Leiter des Lehrstuhls, an welchem auch ich tätig bin), Herrn Prof. Dr. I. KÁRPÁTI (Keszthely), ferner auch den Herrn Dr. A. BORHIDI, Doz. Dr. Sz. PRISZTER, Dr. GY. CZIMBER und P. ERDŐS (OVEF), die mir beim Einsammeln des Lebendmaterials geholfen haben.

Um exaktere Vergleichs- und Differenzierungsresultate zu erzielen, wurden biometrische Messungen vorgenommen. Die Auswahl der Merkmale bzw. Eigenschaftspaare war mit Schwierigkeiten verbunden, weil die zitierten Verfasser den taxonomischen Wert mehrerer Merkmale bestreiten. So haben die Verwertbarkeit der Knollentypen — bis auf DIHORU (l. c.) — nach HRUBY (l. c.) alle (u. a. grösstenteils auch ENGLER) verworfen bzw. in Frage gestellt. Desgleichen wird auch der Länge des Schaftes und des Blattstiels von den meisten Autoren keine besondere Bedeutung beigemessen.

Seine Ansichten über den diagnostischen Wert der einzelnen Organe fasst z.B. DIHORU (l. c. p. 74) folgendermassen zusammen: »Die Blätterform, die Farbe der Blütenscheide und des Anhängsels sind taxonomisch unwichtig, weil sie keine festen Diagneme darstellen« (p. 83). »Es wurden auch andere Diagneme untersucht wie: die Blätterform, die Ringzahl der Blüten, das Verhältnis zwischen der *Osmophorus*- und der Blütenscheidenlänge, zwischen der *Osmophorus*- und der Blütenscheidenfarbe, zwischen der Schaft- und der Blattstiellänge, die Samenzahl der Früchte. Die Deckung der Blütenscheiden- und Blattränder in der Knospe usw. sind aber in der Taxonomie wertlos.« — Naturgemäss haben wir auch von den genannten Merkmalen mehrere gemessen bzw. bewertet.
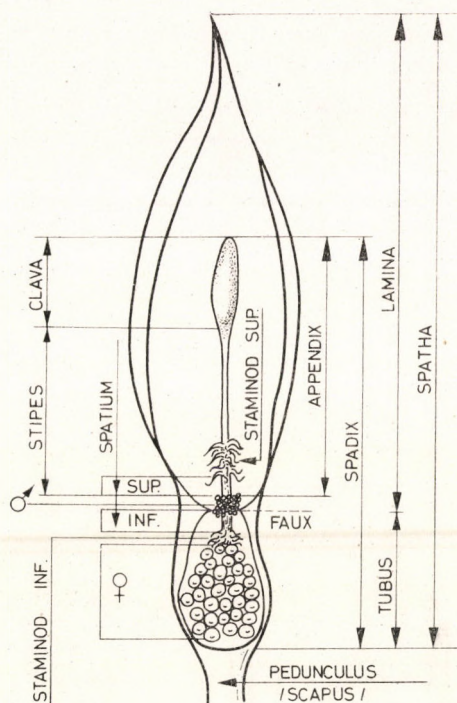
Abb. 1. Erklärung der benützten Fachausdrücke bzw. der Blütenstandsorgane

a) Die untersuchten qualitativen Merkmale

1. Form und Farbe des Rhizoms. 2. Fleckigkeit und Form der Blätter, 3. Farbe der Spatha, des Tubus, 4. Farbe der Antheren, 5. Stellung der Staminodien der sterilen Blüten, 6. Form und Farbe der Keule, 7. Fruchtform.

b) Die untersuchten quantitative Merkmale

Länge des Basislappens des Blattes — Länge des Blattstiels
Länge des Mittelnervs des Blattes — Länge des Schaftes
Länge der Spadix — Länge der Keule
Länge der Spatha — Länge des Anhängsels
Länge und Breite der Frucht

Die biometrischen Messwerte nutzten wir teilweise als Durchschnittswerte, teilweise aber verwendeten wir sie als Relativdaten $\left(\frac{\text{z. B. Pedunculus}}{\text{Petiolus}}\right)$, zur Auftragung von Häufigekeitskurven (wobei auf der Ordinate der Prozentsatz der Häufigkeit, auf der Abszisse die Reihe der relativen Wertklassen zweier Eigenschaftspaare abgetragen wurden. Es wurden Chromosomuntersuchungen durchgeführt.

Zur Verarbeitung der Verbreitung, der Variabilität (Kreuzung) und der phytozönologischen Verhältnisse wurden Standortforschungen durchgeführt.

Übersicht des Schrifttums

Der Komplex *A. italicum* Mill.

Diese Art erwähnt zuerst JÁVORKA (1925: 150—151), u. zw. aus Kroatien, als *A. italicum* f. *neglectum* Townsend. Der Verfasser setzt hinzu, dass *A. italicum* mit dieser Form zu *A. maculatum* hinüberführt. JÁVORKA erwähnt 1937

(p. 53) f. *neglectum* als ein infraspezifische Taxon von *A. maculatum* aus Ungarn (Bakony und Wälder im Komitat Baranya). Die Blätter sind gross, glänzend, hellgrün, wellig, die Aderränder hellgrün, die beiden Blattgründe viel länger als der Hauptnerv der Blattspreite. Der Schaft ist immer kürzer als der halbe Blattstiel; die Spatha gross, weit ausgebreitet, innen lebhaft
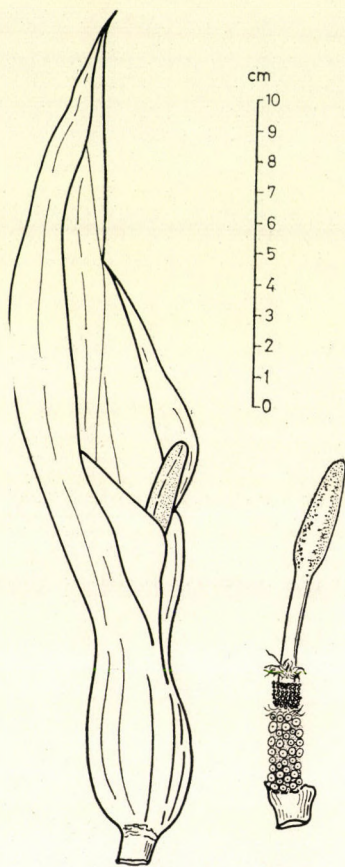
Abb. 2. Arum italicum MILL. aus dem botanischen Garten der Universität für Gartenbau (KE)

grünlichgelb, am Rand oder an der Aussenseite purpurviolett überlaufen. Das sich ausweitende Anhängsel der Spadix ist gelb (fallweise auch purpurn), erreicht aber nie die Mitte der Spatha.

Diese in Süd- und Westungarn vorkommenden Formen mit übergrosser Spatha benannten einige Autoren (HORVÁT, 1942: 48, SOÓ—JÁVORKA, 1951: 974) *A. maculatum* var. *intermedium* Schur. Bemerkt sei hierzu, dass die obenerwähnte Form *neglectum* bereits früher bekannt war; so gab z. B. SIMONKAI (s. N. H.; 1891 No 23692, 1901 No 23690) den an der dalmatischen Küste gesammelten *A. italicum*-Exemplaren die Bestimmung *A. neglectum*.

BORHIDI (in PRISZTER—BORHIDI, 1967: 160—163) hält neuerdings die erwähnte grossspathige *A. maculatum* var. *intermedium* (non SCHUR!) für *A. italicum*, wobei er die folgende Einordnung bietet:

A. italicum Mill. ssp. *concinnatum* (Schott) Engl. in DC. (Syn.: *A. concinnatum* Schott, *A. nickelii* Schott, *A. ponticum* Schott, *A. maculatum* L. var. *intermedium* auct. recent. hung., non SCHUR).

Nach den Autoren wäre die ssp. *concinnatum* ein Übergang zwischen *A. maculatum* und *A. italicum*, gehöre aber schon in den Formenkreis der letzteren. In Ungarn im Westen und Süden Transdanubiens verbreitet.

Noch zwei Übergangsformen verdienen Beachtung, die nach der Form des Appendix eine Zwischenstellung einnehmen: die var. *flavescens* Melzer (ex JANCHEN, 1960: 877) und die subvar. *Tetrelii* Corbière. Beide werden von den betreffenden Verfassern zu *A. maculatum* L. eingeordnet:

f. *flavescens* (Melzer) H. RIEDL (1967: 166),

f. *Tetrelii* (Corbière) TERPÓ (1971).

Das Vorkommen der gelben Keule (clava) ist sowohl im Bakony und im Mecsek als auch an anderen ungarischen Standorten von *Arum maculatum* nicht selten. Das häufige Auftreten der weissen Aderränder, der für die gelbe Keule und für *A. italicum* charakteristischen Merkmale in den Populationen von *A. maculatum* lässt sich auch nach anderen Verfassern (FRITSCH apud RIEDL p. 166; RIEDL l. c. p. 167) mit introgressiver Hybridisation erklären. Zwischen diesen beiden Arten besteht auch heute eine direkte genetische Beziehung; ihre Areale berühren bzw. überdecken sich im südeuropäischen Raum (z. B. auf dem Balkan) häufig.

Arum maculatum und die aus dem Karpatenbecken beschriebenen, lediglich als Synonyme gewerteten Arten

Wir gingen auch hier von einer Mitteilung JÁVORKAS (1925: 151) aus. In seiner Flora Hungarica erwähnt er im Zusammenhang mit *A. maculatum* als Synonym eine ziemlich in Vergessenheit geratene Benennung: *Arum alpinum* SCHOTT et KOTSCHY. In den grösseren Systematiken — so bei ENGLER (1920: 92, *A. m.* subvar. *alpinum*) und bei ASCHERSON—GRAEBNER (1904: 377, *A. m.* B. II. *alpinum*) wird *A. alpinum* nur als infraspezifisches Taxon behandelt. In dieser Frage müssen wir auch die Auffassung SIMONKAIS (1886: 513—514) als massgebend ansehen; bei ihm finden sich die vielfach beschriebenen transsylvanischen *Arum*-Rassen bzw.-Arten *A. sagittaefolium* Benkő, *A. gracile* Unver., *A. intermedium* Schur, *A. maculatum* Baumg., *A. transsilvanicum* Czétz alle als Synonyme von *A. maculatum* var. *alpinum* »zusammengefasst«. Nach einem handschriftlichen Vermerk JANKAS bei SIMONKAI (l. c.) ist die var. *alpinum* auch in der Umgebung von Budapest und Fiume (Rijeka) gemein.

Die aus Siebenbürgen beschriebenen *Arum*-Arten verdanken ihre Publikation der Tätigkeit des namhaften Wiener Arologen SCHOTT. Auch der Verfasser selbst hat viele Taxa gewöhnlich nur auf Spezies-Rangstufe beschrieben. Es ist nun durchaus kein leichtes, sich in den Arten bzw. Formen SCHOTTS zurechtzufinden. Nicht minderes Kopfzerbrechen verursachte das Problem auch RIEDL (l. c.), als dieser das gesamte *Arum*-Material Österreichs verarbeitete. In der weiteren Folge war auch ich selbst der Meinung, dass die *Arum*-Systematisierungsversuche SCHOTTS und seiner Zeitgenossen (FUSS, 1866: 615; SCHUR, 1866: 636; UNVERRICHT, 1854: 173, SIMONKAI, l. c.) nicht ausser acht gelassen werden dürfen gleichviel, ob es sich um Arten oder um infraspezifische Taxa handelt.

Nachdem ich die von den Verfassern beschriebenen, aus diesem Teile Europas belegten Taxa — unter besonderer Beachtung der Fundorte (Verbreitung) — mit dem Herbarmaterial verglichen hatte, kam ich zu der Feststellung, dass im Karpatenbecken mindestens zwei gut unterscheidbare Taxa zu finden sind: die alte Art *A. maculatum* L. (s. s.) und vermutlich *A. alpinum* Schott et Kotschy.

Besonders auf Herbarblättern, deren Belegmaterial gegen Ende des vorigen sowie Anfang dieses Jahrhunderts im Karpatenbecken gesammelt wurde, liest man ausser der Bezeichnung *maculatum* am häufigsten die Bestimmungen *A. alpinum* und *A. intermedium*. Für den grössten Teil des Materials sind die folgenden der bei *A. alpinum* (SCHOTT, 1860: 91) vorhandenen diagnostischen Werte charakteristisch:

»Tuber depressum . . ., lamina fol. sagittata . . ., pedunculus petiolum subaequans . . . Spadix . . . tenuis, vix apicem versus paululo incrassatus . . ., tubus intus atropurpureus . . . Loculis purpureis . . .«

Die Beschreibung entspricht zum Teil den Beschreibungen bzw. Zeichnungen von DOSTÁL (l. c.), HRUBY (1912: 160, Fig. VI), JÁVORKA (1925), JÁVORKA—CSAPODY (1934: Taf. V, Fig. 576/a), SOÓ—JÁVORKA (1951), in denen z. B. die Knolle oval-abgeflacht und nach oben gerichtet, der Schaft $\pm$ gleich lang wie der Blattstiel dargestellt wird.

Arum intermedium Schur unterscheidet sich eigentlich nicht besonders von *A. alpinum* (so findet das auch RIEDL). Halbkugelige, rundliche Knollen entwickelt auch *alpinum* ziemlich selten, weshalb hier von einem infraspezifischen Taxon gesprochen werden könnte.

Erst die früher beschriebene *A. gracile* Unverricht (1854) bildet mit ihrer eher abgeplatteten (diskoiden) Knolle den richtigen Übergang zu den flachknolligen orientalischen Arten (z. B. *A. orientale* M. B.), ist aber noch der taxonomischen Einheit *A. alpinum* zuzurechnen.

Hier möchte ich schliesslich noch die Vorschläge RIEDLS (1967: 164) zur infraspezifischen Gliederung von *A. maculatum* anführen. Dieses System wäre

noch durch die von PRIME (1961: 108) differenzierte, in Dänemark bodenständige Subspecies *danicum* zu ergänzen. Das System RIEDLS zeigt wesentliche Unterschiede gegenüber der ENGLERschen *A. maculatum*-Gliederung und schenkt auch den mittel- und ostmitteleuropäischen Formen grössere Beachtung.

A. maculatum 1. subsp. *maculatum*
a) var. *maculatum*
b) var. *immaculatum* (Syn. *A. besserianum* Schott, *A. maculatum* subsp. *danicum* Prime)
f. *roseum* Gremblich
f. *flavescens* (Melzer) H. Riedl
2. subsp. *alpinum* (Schott et Kotschy) H. Riedl

Das Verhältnis zwischen *A, maculatum* L. und *A. orientale* M. B. (s. l.)

Die erste Mitteilung über *A. orientale* M. B. verdanken wir JANKA (ÖBZ XIII. 114) mit dem Fundort Székelyhíd (= Săcuieni, Siebenbürgen) im Komitat Bihar. NEILREICH (1866: 72) berichtet — an JANKA anknüpfend — über *Arum orientale* ebenfalls aus den Wäldern von Székelyhíd sowie aus der Umgebung von Grosswardein (Nagyvárad = Oradea), bemerkt jedoch, dass sich diese Form von *A. maculatum* kaum etwas unterscheidet. Neuerdings beruft sich in dieser Hinsicht auch DIHORU (l. c.) auf JANKA. Ich selbst hatte Gelegenheit, aus Székelyhíd stammendes Herbarmaterial zu sehen. Nach meiner Ansicht wäre diese Pflanze von JANKA in den Formenkreis *gracile-intermedium* einzureihen. Ähnliche Pflanzen wachsen auch anderwärts in Siebenbürgen, so in der Gegend von Gánts (Ganţiu) (HAYNALD N. H.) und Monora (Mănărade) (J. BARTH WRO. H.).

Was das Gebiet Ungarns anbelangt, berichtet SIMKOVICS (1878) aus der Gegend von Debrecen, RICHTER (1871) aus Budapest (Lipótmező = Leopoldsfeld i. d. Budaer-Bergen) über Vorkommen von *A. orientale*. Beide Stellen sind Standorte von *A. alpinum.*

In der Walachei dürfte *A. orientale* auch in früherer Zeit häufiger gewesen sein (GREGESCU, 1898: 641), heute ist es nach DIHORU in Rumänien ziemlich verbreitet.

Hier ist es wohl angebracht, die taxonomische Stellung und die Verwandtschaftsbeziehungen des gleichfalls stark umstrittenen *Arum besserianum* zu berühren. Die Mitteilungen von SZAFER (1914: 72, Fig. 2), Fig. 2), VISJULINA (1936: 37—41, Fig. 1; 1950: 12—14) sowie Einsichtnahme in das Herbar der Krakauer Jagello-Universität ermöglichten es mir, die Form *besserianum* näher kennenzulernen. Diese Pflanze kommt in Südpolen und in der Ukraine

(Podolischer Rücken) vor; Blütenstand, Blattstiel (kürzerer Pedunculus), längere, eher zylindrische Keule und grünlichweisse Spatha lassen eine nähere Beziehung zum Formenkreis *A. maculatum*, die diskoide, in der Regel jedoch schief gestellte Knolle hingen, eine Beziehung zu *A. orientale* vermuten. Ihre Zwischenstellung betont auch SZAFER (im zitierten Beitrag).

Standortuntersuchungen

Die Forschungen im natürlichen Gelände spielten — vor allem beim Auseinanderhalten der Taxa von der Rangstufe species — eine sehr wichtige Rolle. Waren bei ENGLER (l. c. p. 87) für *A. maculatum* noch dreierlei Knollen kennzeichnend (»Tuber plerumque ovoideum vel cylindroideum, rarius [locis petrosis] discoideum«), lieferten die an der Elbe und in Ungarn durchgeführten Knollenausgrabungen den Beweis dafür, dass jeder Art nur einerlei Knollenform eigen sein kann (selbst unter Beachtung der natürlichen Variabilität).

Abb. 3. Rhizome von *Arum maculatum* L. aus der Gegend von Bakonygyepes (leg. M. POMOGYI-TERPÓ et A. TERPÓ)

Die Erkenntnis des grossen diagnostischen Wertes des Rhizomtyps beschleunigte ganz erheblich auch die Abgrenzung der Verbreitung der Taxa.

An Hand der ausgegrabenen Knollen liesse sich die Westgrenze des zur Donau hin verlaufenden Areals etwa so abstecken: von Mosonmagyaróvár quer durch den Bakony (Zirc-Veszprém), am Westufer des Plattensees entlang mit Berührung von Keszthely, sodann nördlich von Kaposvár zwischen Szekszárd und dem Mecsek-Gebirge (l. c. TERPÓ). Westlich von dieser Linie wuchsen *Arum* Pflanzen, die sich aus zylindrischen, gewöhnlich horizontal gelagerten, rhizomartigen Knollen entwickelten, östlich von dieser Grenzlinie fanden wir Pflanzen mit ovoid-abgeplatteten, hochgerichteten Knollen. Besonders auf dem zylindrischen Rhizom (z. B. im Bakony) kam es zu einer so übermässigen Bildung von Tochterknollen (s. TERPÓ, l. c.), dass die Pflanzen nicht einzeln, sondern gruppenweise wuchsen. (Die sonstigen wissenschaftlichen Resultate der Standortuntersuchungen — z. B. die zönologischen Bearbeitungen — bleiben einer späteren Veröffentlichung vorbehalten.)

Zytologische Daten

Der Rhizomform massen wir eine grössere Bedeutung bei, als es bisher üblich war, u. zw. bereits im Vorbereitungsstadium der Chromosomen-Untersuchungen, waren wir uns ja dessen bewusst, dass in der Literatur bei den einzelnen *Arum*-Arten — so u. a. auch bei *A. maculatum* — mehrere Chromosomenrassen verzeichnet.

Schon anfangs — beim Sammeln der Belege — sortierten wir das Material nach den zweierlei Knollentypen (sofern die beiden Arten nebeneinander wuchsen) und bereiteten es für die Anwurzelung vor. Die Chromosomenzahl der Pflanzen mit oval-abgeplatteten, nach oben gerichteten Knollen betrug 28, die des Knollen mit zylindrischem Rhizom dagegen 56.

Die Chromosomenwerte der behandelten *Arum*-Arten sind, nach Verfassern geordnet:

DARLINGTON (1957)

Arum × =	14, 16
	28
maculatum	56, 84
italicum	64

OBERDORFER (1962: 205)

A. maculatum	
var. *immaculatum*	2n = 28
var. *maculatum*	2n = 56

TARNAVSCHI (1948: 26)

Arum L. × = 7; *Arum maculatum* L.: 14 HAGERUP 1942; 16 SCHMUCKER 1925; 28, 42 MAUDE 1939, 1940

Löve A.—Löve D. (1961: 34)

Arum L. × = 7,	(8)	
maculatum L. s. str.	56	Maude 1939, 1940, Hagerup 1944a, Baker (in Sowter 1949), Lovis 1954, Prime 1954, 1955
immaculatum Rchb.	28	Hagerup 1944a (und in L. et L. 1942b)
italicum Mill.	84	Maude 1939, 1940; Lovis 1954, Prime 1954, Jones 1957, cf. Prime, Buckle and Lovis 1955
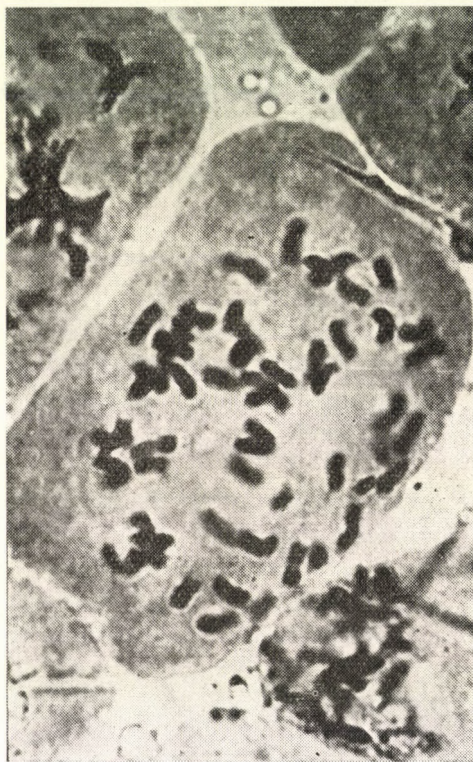
Abb. 4. Chromosomen von *Arum maculatum* (Bakonygyepes)

Bolkhovskikh—Grif et al. (1960: 50)

A. albispathum Stev.	56	Zakharyeva, Makušenko 1968
korolkowii Regel	28	Zakharyeva, Makušenko 1968
neglectum (Townsend)	83, 84	Prime 1954, P. et al. 1955
nigrum Schott		Gori 1957 (I. 1958)
var. *apulum* Carano	56	
orientale M. B.	28	Zakharyeva, Makušenko 1968

Wie DIHORU mitteilt, wurde der Chromosomensatz von zwei *Arum*-Arten auch in Rumänien untersucht (I. LUNGENAU apud DIHORU):

A. orientale (aus der Umgebung von Bukarest)	28
A. maculatum (aus Oltenien)	56

PRIME (1961) gelang es, eine neue diploide Unterart von *A. maculatum* (Chromosomenzahl 56), u. zw. *A. m.* subsp. *danicum* Prime ($2n = 28$) in Dänemark abzugrenzen.

Abb. 5. Chromosomen von *Arum alpinum* (Csatka, Koromla psz., im Bakony-Gebirge)

Unsere eigenen Untersuchungen erstreckten sich auf *A. maculatum* und *A. alpinum*. Von jeder Art verschaffte ich mir — von je zwei Orten — Rhizome als Untersuchungsmaterial: 1. *A. maculatum*-Rhizome aus der Gegend von Dessau (an der Elbe, in der DDR) und aus dem Bakony-Gebirge (Bakonygyepes); 2. *A. alpinum* von den östlichen Ausläufern des Bakony und aus dem Wald Tőserdő bei Lakitelek an der Theiss. Die Chromosomenzahl betrug bei

A. maculatum (beide Fundorte)	56
A. alpinum (beide Fundorte)	28

Taxonomische Folgerungen

Die Absonderung von *A. italicum* bereitet trotz der unterschiedlichen Mitteilungen keine besonderen Schwierigkeiten. Diese Art treibt Jahr für Jahr im Herbst (August—September) Blüten (sie kennt nur eine Ruheperiode, u. zw. im Sommer!), ihr Rhizom ist braunrot, die Keule recht gross (3,0—7,0 cm lang, 0,3—1,0 cm dick) und gelb gefärbt; die Chromosomenzahl 2n = (64), 84 deutet auf eine nahe verwandte, aber auch geographisch abgegrenzte Art hin.

Vergleicht man die beschriebenen (TERPÓ, 1971) und am Standorte untersuchten Populationen von *A. maculatum* var. *maculatum* mit dem LINNÉschen Typ dieser Art, muss man jedenfalls eine charakteristische Gruppe annehmen, die im engeren Sinn jener entspricht (z. B. Spadix kürzer als die halbe Spatha, der Schaft kürzer als der Blattstiel, Knolle zylindrisch, rhizomartig). Als Besonderheit kann man die Tatsache werten, dass in fast jeder Population auch Exemplare mit violettschwarz gefleckten Blättern vorkommen. Populationen von solcher Zusammensetzung haben die Chromosomenzahl 2n = 56, was auch von der überwiegenden Mehrheit der angeführten Autoren bekräftigt wird.

Eigenartig und überraschend ist das Bild, das sich aus der Gegenüberstellung der Chromosomenzahlen bei den an den Blättern ungefleckten (morphologisch im Grund unterschiedlichen), jedoch für *A. maculatum* L. gehaltenen Pflanzen ergibt. Die Verfasser geben die Chromosomenzahl der var. *immaculatum* fast durchwegs mit 2n = 28 an.

Auf meinem Untersuchungsareal konnte ich zwei Typen mit ungefleckten Blättern differenzieren. Das eine Taxon — *Arum maculatum* L. var. *immaculatum* Reichenbach — kommt immer im Areal von *A. maculatum* vor; in den übrigen morphologischen Merkmalen — die Spadix kürzer als die Hälfte der Spatha, der Schaft kürzer als der Blattstiel, der Wurzelstock ein horizontal langgestrecktes Rhizom, die Staubblüten gelb usw. — ist es identisch mit der var. *maculatum*, 2n = 56. Das zweite, in grösserem Umfang östlich vom Verbreitungsareal des *A. maculatum*, auch im Karpatenbecken vorkommende, an den Blättern ungefleckte Taxon ist *A. alpinum* Schott et Kotschy. Bei ihm ist die Spadix länger als die halbe Spatha, der Schaft ist ± ebensolang wie der Blattstiel, den Wurzelstock bildet ein schräg aufwärts stehendes, ovoid abgeplatteter Knollen, die Staubblätter purpur-lila, 2n = 28 usw.

Von den siebenbürgischen *Arum*-Taxa habe ich die auch in anderen Teilen Europas gelegentlich vorkommende *A. intermedium* als Varietät gewertet. Die eher rundlichen oder halbkugelförmigen Knollen dieser Pflanze findet man auf den meisten Standorten; in den übrigen Merkmalen ist die Pflanze völlig identisch mit *A. alpinum* (s. auch bei RIEDL l. c.). Das bisher meist fälschlich als *intermedium* bestimmte, nur in Siebenbürgen vorkom-
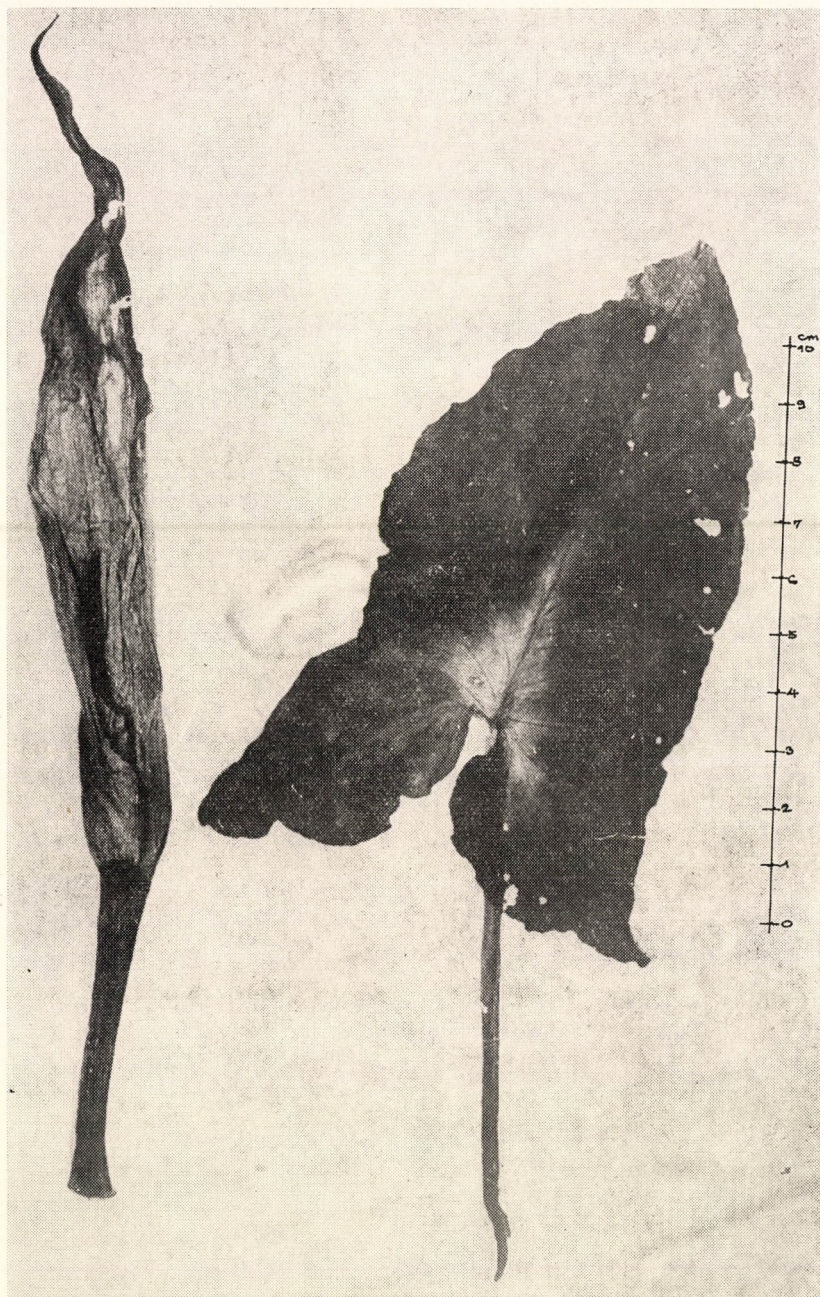
Abb. 6. LINNÉscher Typ von *Arum maculatum.* Aufnahme v. S. M. WALTERS (H. Univ. Cambridge). Schaft sehr kurz; die Pflanze gehört zu den Formen mit grösserer Spatha (16—17 cm), das Blatt ist sehr kennzeichnend

mende *A. gracile* würde ich vorschlagen, als Subspecies von *A. alpinum* einzuordnen. Der östliche Nachbar von *alpinum*, das *A. orientale* M. B. ist eine Pflanze des Balkans, Ostrumäniens und weiter der Südukraine sowie des Kaukasus.

Im Areal von *A. alpinum* — in den östlichen und nordöstlichen Randgebieten der Karpaten — gibt es sich schärfer abhebende Taxa, u. zw. in Gestalt des *gracile* sowie des *A. besserianum*. Dies könnte zugleich auch bedeuten,
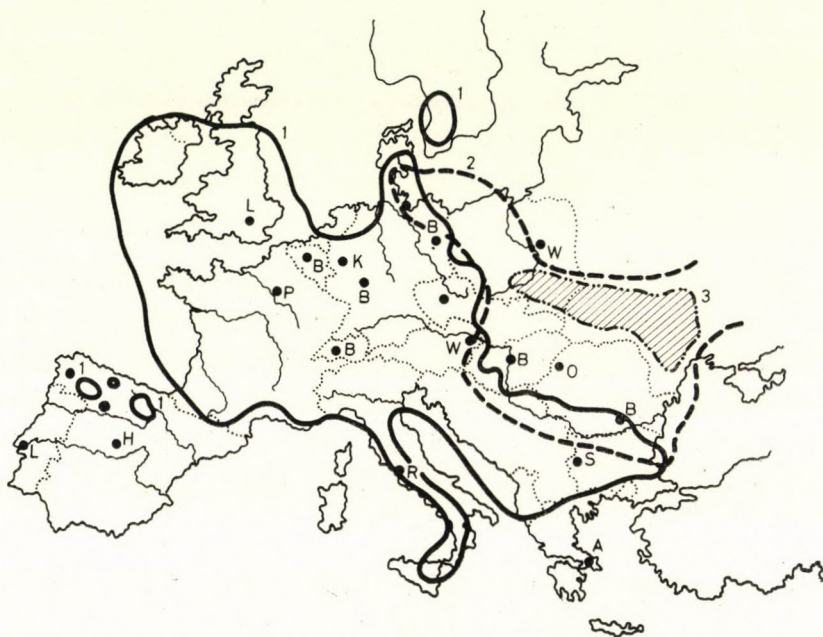
Abb. 7. Verbreitung von *Arum maculatum* (1) (Abänderung nach MEUSEL), *Arum alpinum* (2) und von (3) *A. besserianum* (Original: TERPÓ)

dass ihre Verwandtschaft mit den östlichen Rassen bzw. Arten tiefer begründet ist. In der östlichen Hälfte ihres Areals sind sogar mehrere diploide (2n = 28) Rassen — z. B. A. *orientale*, *A. korolkowii* — zu finden.

An der im Karpatenbecken entlangstreichenden Arealgrenze von *A. maculatum* sind — wenn auch in geringerem Masse — auch Kreuzungsformen mit *A. alpinum* zu beobachten. Solche Exemplare haben einen langen Schaft, oft lila Staubblätter, eine schräge-ovoide Knolle u. dgl. Als Ergebnis meiner Untersuchungen habe ich ein hybridogenes Taxon beschrieben und ihm den Namen *Arum* × *Soói* gegeben.

6.1. Übersicht der Taxa

I. *Arum italicum* Mill. (1768)

II. *Arum maculatum* L. (1753) emend. Mill. (1768)
1. var. *maculatum*
f. *maculatum*
f. *Tetrelii* (Corbière, 1898) Terpó (1971)
f. *flavescens* (Melzer, 1960) H. Riedl (1967)
f. *spathulatum* Terpó (1971)
2. var. *Kárpátii* Terpó (1971)
3. var. *angustatum* Engler (1879)
f. *angustatum*
f. *parvulum* (Borhidi, 1967) Terpó (1971)
f. *scolopendriforme* Priszter (1949)
f. *roseum* (Gremblich, 1920) H. Riedl (1967)
4. var. *immaculatum* Reichenbach (1830)

III. *Arum alpinum* Schott et Kotschy (1851), emend. Terpó (1971)
a, subsp. *alpinum*
1. var. *alpinum*
f. *alpinum*
2. var. *pannonicum* Terpó (1971)
f. *pannonicum*
f. *Jávorkae* Terpó (1971)
3. var. *intermedium* (Schur, 1860) Terpó (1971)
b, subsp. *gracile* (Unverricht, 1854) Terpó (1971)
c, subsp. *danicum* (Prime, 1961) Terpó (1971)

IV. *Arum* × *Soói* Terpó (*A. alpinum* × *A. maculatum*) (1971)

V. *Arum besserianum* Schott (1858)
f. *besserianum*
f. *miodoborense* (Szafer, 1914) Terpó (1971)

VI. *Arum orientale* M. B. (1808), emend. Engler (1878)
a. *Arum orientale* M. B. (1808) s. str.
b. *Arum elongatum* Stev. (1856)

Beschreibung der wichtigsten Taxa*

I. *Arum italicum* Mill. Dict. ed. 8. (1768) n. 2. Im Karpatenbecken künstlich angepflanzt. Natürliches Verbreitungsareal: Mittelmeergebiet und Westeuropa (s. noch Terpó 1971).

II. *Arum maculatum* L. Spec. pl. ed. 1. p. 966 (1753) emend. Mill. Gard. dict. ed. 8. (1768). Das in der Erde befindliche Organ ist ein länglicher (gewöhnlich horizontal liegender) Knollen. Der Blütenschaft ist kürzer als der Blattstiel, die Blätter lila-schwärzlich gefleckt; die Spatha im allgemeinen grünlichweiss, die Spadix reicht nicht über die Mitte der Spatha hinaus; die Antheren sind gelb; die Frucht stumpf, abgekappt aussehend. Die Pflanze treibt im Frühling aus. Verbreitung auf dem untersuchten Areal: Österreich, Tschechoslowakei (Böhmen), Jugoslawien, Ungarn (westliche u. südwestliche Teile von Transdanubien), Rumänien (südlich der Mieresch [Maros = Mureş]). Einige Fundorte:

* Eine ausführlichere Beschreibung der Formen von *A. maculatum* ist in Botanikai Közlemények (1971: 150—160) enthalten.

Abb. 8. Blütenstand von *Arum maculatum* mit purpur-lila Spadix (Mosonmagyaróvár, Foto: TERPÓ)
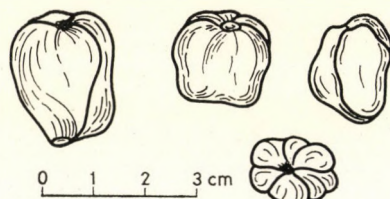
Abb. 9. Früchte von *Arum maculatum* (Dessau, an der Elbe)

Tschechoslowakei (Böhmen, ohne Mähren):
PRU. H.: Litomyšl (B. FLEISCHER, 1905); Pardubice (J. KOSTÁL, 1894); Vysoké Mýto (B. FLEISCHER, 1905); Č. Středohoři: Tellnitz (Telnice) (J. SCHUBERT, 1885); Kadaň (KRATZMAN); — WRO. H.: Teplice (M. WINKLER, 1852).

Jugoslawien:
U. H.: Kamenica: Fruška Gora (BERNÁTSKY, 1904; BANITZ, 1904); Sombor (= Zombor) (PRODAN, 1908); **D. H.:** Deliblát (MÁGÓCSY-DIETZ, 1913); Werschetz (Versec = Vršac) (A. RICHTER, 1891); Fiume (=Rijeka) (FILARSZKY—KÜMMERLE—MOESZ, 1907); **N. H.:** Klek (SIMONKAI, 1893); Ogulin (SIMONKAI—THAISZ).

Ungarn (Transdanubien):
Bakonyicum: **D. H.**: Somlóvásárhely (Kulcsár—Vozáry, 1953); **N. H.**: Bakony-Gebirge: Bakonybél (Simkovics, 1870; Soó, 1955, **U. H.**); Pápasalamon (Jávorka—Tallós—V. Csapody, 1955); Bakonygyepes (Frau Pomogyi-Terpó—Terpó, 1968, **KE. H.**); Fenyőfő: Cuha-völgy (Gyepesi, 1900). Praenoricum: **N. H.**: Sárvár (V. Csapody—Pénzes, 1964; Retkes, Frau Pomogyi-Terpó—Terpó, 1969, **KE. H.**); Sorkikápolna (Márton, 1891; Takátsy, 1969, **KE. H.**). Eupannonicum: Arrabonicum: **KE. H.**: Kimle—Mosonmagyaróvár—Halászi—Feketeerdő (Czimber—Erdős—Frau Pintér—Terpó, 1968); Répcelak—Rábakecöl (Frau Pomogyi-Terpó—Terpó, 1969);
Praeillyricum: **N. H.**: Mecsek-Gebirge: Hosszúhetény (Jávorka, 1930); Pécs: Misina—Tubes: (Vajda, 1931; V. Csapody, 1955); **U. H.**: Mecsek-Gebirge: Tubes (Borhidi—Priszter, 1966); Pécsvárad: Zengő (Soó, 1936); Villányer Gebirge: Bisse (Borhidi—Priszter, 1966); Nagyharsány (Soó, 1966); **N. H.**: Komitat Somogy: Szőkedencs (J. Keller, 1943); Csurgónagymárton (Jávorka, 1938); Kaposmérő: Ráspolyerdő (Jávorka, 1938); **KE. H.**: Mecsek-Gebirge: Misina (Horvát—Terpó, 1969); Kisvaszar (Horvát—Terpó, 1968).

Rumänien (Siebenbürgen):
U. H.: Kronstadt (Brassó = Brașov) (Kümmerle, 1903); **N. H.**: Hevis (Barth, 1862); Zam (Barth, 1877); Arad (Simonkai, 1885); Domugled (Pax, 1912); Herkulesbad (Herkulesfürdő = Băile Herculane) (Pax, 1879, Bohatsch).

Entferntere Fundorte:

Deutschland:
HAU. H.: Strassburg (G. Zahn, 1880); Erzgebirge (Batsch, M. Dietrich); Erfurt (Reinecke, 1916); Weimar, Magdeburg (Anonym, 1825); Leipzig (Goetz); Heidelberg: Schlossberg (Bauche 1872); Baden (Hoffmann, 1877); Gera (Kaufmann, 1888); Mühlheim (C. Haussknecht, 1860); Rogatz (John); Rhein Markt (J. Walter, 1938); **PRU. H.**: Zwickau (A. Lehmann, 1906); München (C. O. Hara); **U. H.**: Neuburg (W. Gugler, 1903, **U. H.**), Görlitz (C. Rabnitz, **N. H.**)

Schweiz:
HAU. H.: Kaiserstuhl (R. Sturenberg, 1929).
England:
J. H.: Surrey: Mertham (S. Baroko, 1945).

III. *Arum alpinum* Schott et Kotschy in Mohl u. Schlechtendal, Bot. Zeit. p. 285—286, 1851, emend. Terpó. — Schott, Prodr. p. 91—92 (1860); Schott, Synopsis p. 12 (1856); Fuss, Fl. Transsilvaniae p. 615 (1866); Schur, Enum. p. 636 (1866).

Syn.: *A. immaculatum* Schott 1856: 92 p. p. *A. transsilvanicum* Czetz 1872: 11 p. p. *A. maculatum* var. *immaculatum* p. p. auct. et collect. *A. maculatum* B. II. *alpinum* Ascherson et Graebner 1904: 376, *A. maculatum* var. *alpinum* Simonkai 1886: 514, p. p., auct. et collect. Trans. plur. *A. maculatum* var. *β angustatum* subvar. *alpinum* (Schott et Kotschy) Engler 1920: 92, *A. maculatum* subsp. *alpinum* H. Riedl 1967: 159—168, *A. maculatum* Jávorka 1925: 150—151 p. p. et auctorumque collect. hung. plur. *A. orientale* auct. et collect. hung. trans. non M. B., Dihoru 1970: 82—84 p. p.

Tuber depressum, ovoideum erectum. Lamina fol. sagittata 9,0—12,5 (14,0) cm longa et 6,0—8,0 (10,0) cm lata; vena media 8,0—10,0 cm, vena lobi 4,0—5,0 (7,0) cm longa: petiolus 25,0—30,0 cm longus. Pedunculus petiolum aequans, subaequans vel rarius superans. Spatha oblongo-lanceolata, 8,0—12,0 (25) cm longa, virescens vel margine sordide vel violaceo-purpurascens; tubus intus excepto imo albo, purpureus. Spadix mediam laminam superans, 4,0—6,5 cm longus. Appendix longe-stipitata, stipite cylindrico; clava tenui stipitem aequante, paululo incrassata vel fusiformis, oblongo-ovata, obtusa 0,7—2,0 cm longa et 0,2—0,7 cm crassa, pallide violacea quam stipes 2-plo breviore. Stamina violacea. Florum sterilium rudimenta tenuiter filamentosa, superiora plerumque (3) 4—5 (10) cycla, inferiora oligo 2— (3) cycla. Bacca oblongo ovoidea, obtusa. Chromosomata 2n = 28.

Die Pflanze besitzt abgeflacht-eiförmige, etwas schief nach oben gerichtete, elfenbeinfarbene Knollen. Der untere Kreis der Staminodialblätter entwickelt sich gewöhnlich nur 0,2—0,3 cm über dem höchsten Kreis der männlichen Blüten, ihre überhängenden Haare erreichen dabei die Staubgefässe.

Die weiblichen Blüten sind ovoid ± horizontal abstehend. In der roten Frucht bilden sich 1 bis 4 hellgelbe Samen mit geriffelter Schale.

Lectotypus: Budapest: in silvaticis montis János-hegy, 19. V. 1906; leg. FILARSZKY, KÜMMERLE et JÁVORKA; in Herb. Mus. Nat. Hungar. Budapest No 23 743/91.
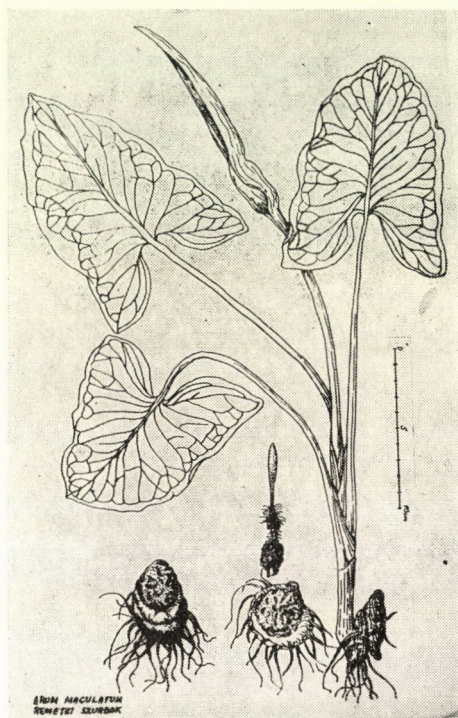
Abb. 10. Arum alpinum var. *pannonicum*, Budaer Gebirge (leg. A. TERPÓ)

Infraspezifische Taxa

a) subsp. *alpinum* — tuber depressum; ovoideumque erectum; spatha virescens 8,0—12,0 cm longa margine sordide vel violaceo-purpurascens; spadix spathae mediam laminum superans.

1. var. *alpinum* (Syn.: *A. maculatum* var. *β angustatum* subvar. *alpinum*); clava tenui stipitem aequante; spatha virescens, margine sordide vel violaceo purpurascens.

f. *alpinum* — lamina fol. sagittata, clava tenui. Verbreitung: **OV. H.** BANAT: Werschetz = Versec = Vršac (WAGNER, **HAU. H.**) **WRO. H.** Im Kasan: Plawtschewitza (DEGEN, 1904; dieses Belegexemplar definierte ENGLER als *A. m.* var. *β angustatum* ENGL. subvar. *alpinum*); Mehadia (RICHTER A., 1910, **HAU. H.**); TRANSSILVANIA: Monora = Mănărade (BARTH, 1873, **HAU. H., J. H.**); Nagyenyed = Aiud = Strassburg: an der Mieresch (CSATÓ,
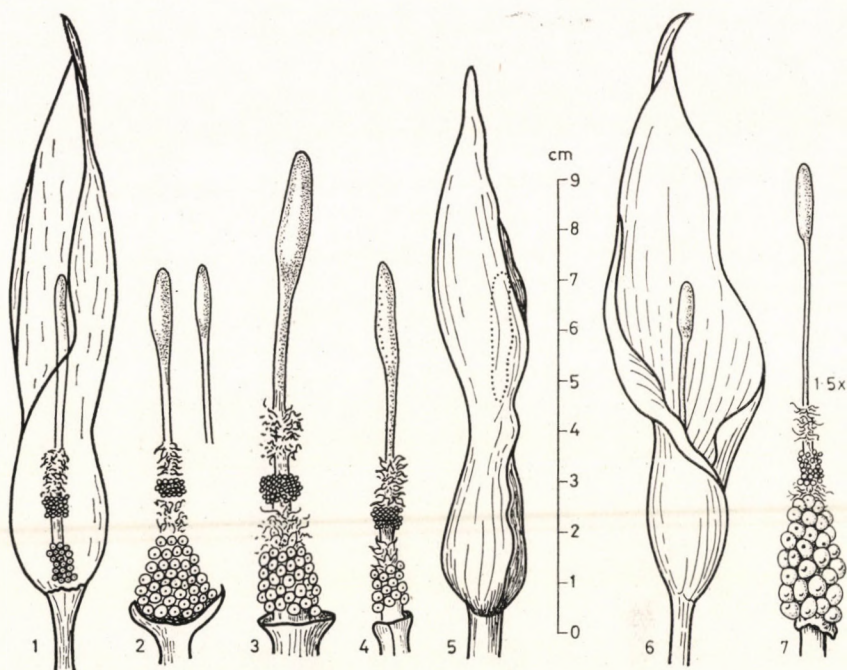
Abb. 11. Blütenstände von *Arum alpinum.* 1) var. *alpinum*, Budaer Gebirge (N. H.: N° 23 696), var. *pannonicum:* 2) Sopron (N. H.: N° 23 790), 2—5) Csatka-Koromla (Bakony-Geb.), 6—7) Debrecen, leg. Soó
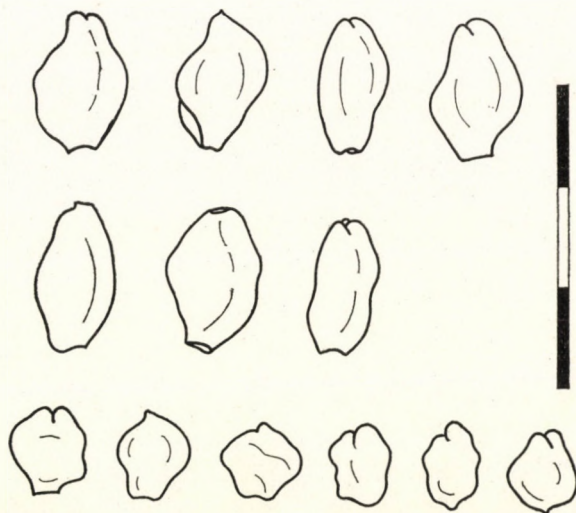
Abb. 12. Früchte von *A. alpinum* var. *pannonicum*, Nagygeresd (Westungarn)

1883, HAU. H.); EUPANNONICUM: Lakitelek: Tőserdő (an der Theiss = Tisza) (BERKI—TERPÓ, 1972). BAKONYICUM: Ofner Berge: Széchenyi-hegy (Svábhegy = Schwabenberg (VAJDA, 1935, N. H.), Vadaskert, Hűvösvölgy (FILARSZKY, 1906, N. H., 1913, OV. H.).
Polen: Ojców (S. KOZŁOWSKI, J. H.).

2. var. **pannonicum** Terpó var. nov.

Spatha virescens vel margine violaceo-purpurascens; tubus intus purpureus; clava pallide-violacea fusiformis vel oblongo obtusula plerumque longe-
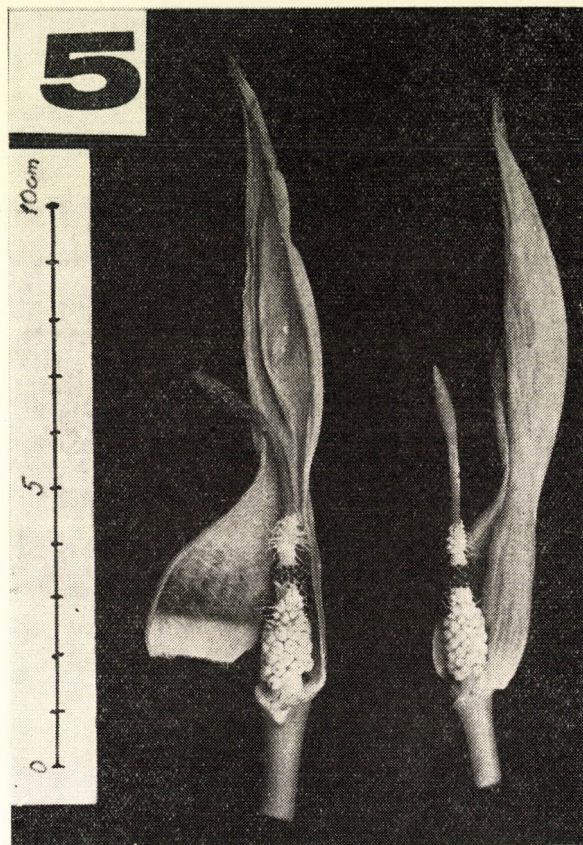
Abb. 13. Arum alpinum var. *pannonicum*, Mosonmagyaróvár. Auf dem Bild sieht man deutlich die Innenfärbung des Tubus und die purpur-lila Farbe der Antheren

stipitata a basi attenuata, 1,2—2,5 cm longa, 0,3—0,6 cm crassa. A var. *alpino* differt clavis crassiusculis fusiformibusque; a var. *intermedio* differt tuberibus ovoideis erectis.

Allgemein verbreitet hauptsächlich auf dem Gebiete der pannonischen Florenprovinz.

Holotypus: HUNGARIA occ.: EUPANNONICUM: Mosonmagyaróvár: an der Leitha (= Lajta) 1969, leg. CZIMBER—ERDŐS—TERPÓ (N° 14 475, **KE. H.**): paratyp.: N° 18 224, 14 472.

f. *pannonicum* — Spatha virescens, vel margine violaceo-purpurascens clava pallide-violacea fusiformis, longe stipitata; tuber depressum, ovoideumque erectum.
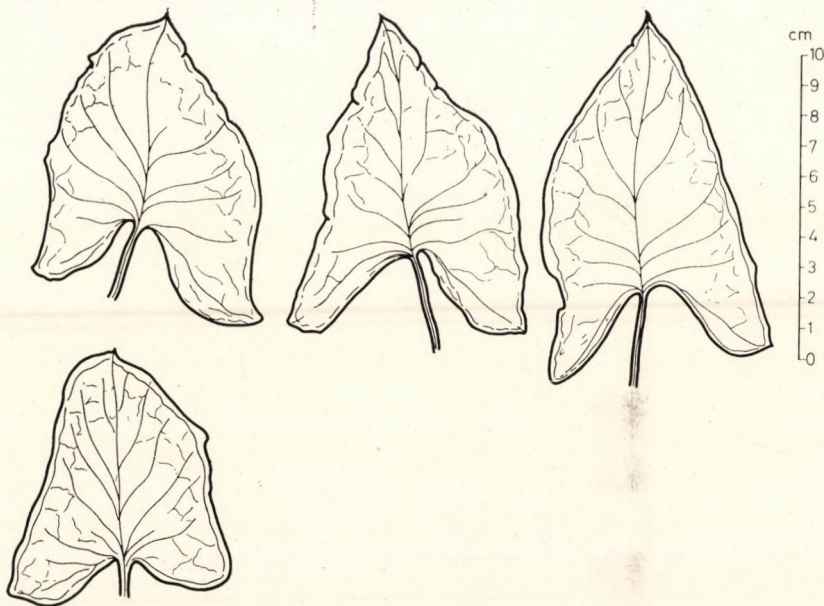
Abb. 14. Arum alpinum var. *pannonicum* f. *pannonicum*, Kimle—Mosonmagyaróvár (Westungarn), KE. H.: leg. M. POMOGYI-TERPÓ et A. TERPÓ

EUPANNONICUM: Hung. bor.-occ.: Mosonmagyaróvár: an der Leitha (= Lajta) und im Lóvárer Wald (CZIMBER—ERDŐS—TERPÓ, 1969), DUNASZIGET: (Frau POMOGYI-TERPÓ—TERPÓ, 1970), Kimle: an der Mosoner Donau (Donauarm von Moson) (POMOGYI—TERPÓ, 1969); Nagygeresd (Frau POMOGYI-TERPÓ—TERPÓ, **KE. H.**) **D. H.**: Csévharaszt (SIMON—HORÁNSZKY); Hencida (KOVÁCS, 1935); Geszt (SOÓ, 1947).
PRAENORICUM: **N. H.**: Sopron (23 723, 23 790); Sorokpolány (TAKÁTSY, 1968, **KE. H.**); Egyházasfalu (Frau POMOGYI-TERPÓ—TERPÓ, 1969).

f. **Jávorkae** Terpó f. nov.

Spatha virescens, vel margine violaceo-purpurascens, lamina fol. acuminata, hastata. — Dedicavi in honorem Acad. S. Jávorka.

Holotypus: BAKONYICUM orient.: Csatka-Koromlapsz., 1969, leg. Frau TERPÓ-POMOGYI—A. TERPÓ—LINK (N° 14 471, **KE. H.**); paratyp. N° 18 199, 15 575, 18 209; Vértes-Gebirge: Tatabánya (Frau POMOGYI-TERPÓ—Frau PINTÉR—A. TERPÓ, 1969) — Areal: Bakony und Vértes-Gebirge.

3. var. **intermedium** (Schur) Terpó comb. et stat. nov.

Syn.: *A. intermedium* Schur ex Schott 1860: 91; Schur, Enum. p. 636 (1866). *A. Besserianum* et *A. orientale* auct. Hung. *A. orientale* Dihoru (l. c.) p.p. Abbildungen: Icon. Herb. Mus. Pal. Vind. N° 1278—80: *A. intermedium* Schur.
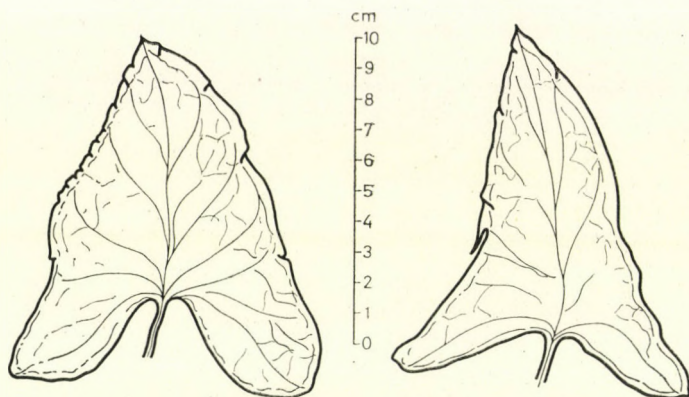
Abb. 15. Arum alpinum var. *pannonicum* f. *Jávorkae*, Csatka—Koromla (im östl. Bakony-Gebirge), KE. H.
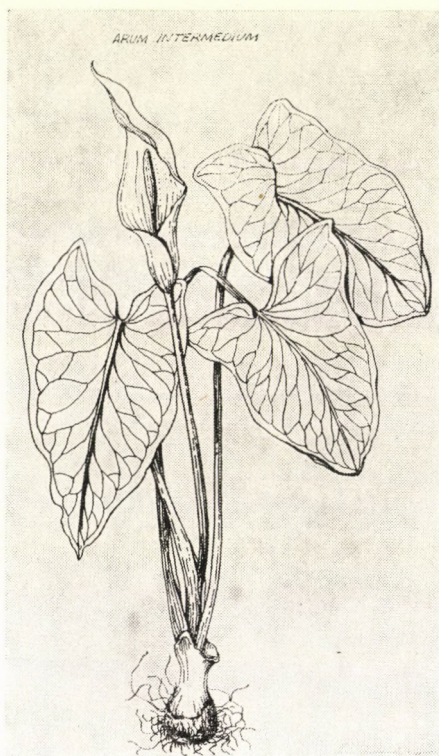
Abb. 16. Arum alpinum var. *intermedium*. Kopie aus dem Nachlasse SCHOTTS

Tuber rotundatum, hemisphaericum plerumque a latera adnatus. Lamina fol. $\pm$ hastato-sagittata. Clava incrassata, subconoidea obtusa. A var. *alpino* differt clavis crassiusculis foliis hastato-sagittatisque et tuberibus rotundatis, a var. *pannonico* tuberibus rotundatis.

Der Appendixstiel unterscheidet sich deutlich von der oblong-spindelförmigen bzw. zylindrischen Keule, der Stiel selbst ist ebensolang wie die Keule oder länger als diese.

Verbreitung: innerhalb des *alpinum*-areals sporadisch überall, z. B. in Rumänien, in Österreich (H. RIEDL l. c.), in Jugoslawien und auch in Ungarn. Wahrscheinlich gehört die im Beitrag DIHORUS (l. c. p. 53) für *A. orientale* gehaltene, in Ungarn im Bükk-Gebirge (Rejtek, 550 m Seehöhe) gesicherte Pflanze auch hierher. Hingegen sind die in den vierziger Jahren als *A. maculatum* var. *intermedium* bezeichneten Pflanzen ungarischer Provenienz nicht hierherzurechnen (s. die Synonyme von *maculatum!*).
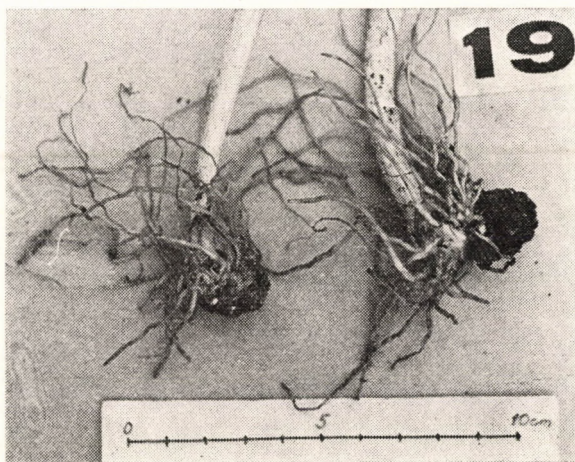
Abb. 17. Arum alpinum var. *intermedium*, aus der Gegend von Mosonmagyaróvár (Westungarn)

Fundorte: EUPANNONICUM: Mosonmagyaróvár entlang der Leitha (= Lajta) Lóvárer Wald (N° 18 468, 18 471, 18 469, 15 542, 13 080 CZIMBER—ERDŐS—TERPÓ); BAKONYICUM: Csatka-Koromla (Frau POMOGYI-TERPÓ—A. TERPÓ, **KE. H.**).

Übersicht über die Fundorte des Formenkreises von ssp. *alpinum*

In Ungarn

CARPATICUM: **N. H.**: Sátor-hegység (Sátor-Gebirge): Sátoraljaújhely (SOÓ, 1938); Füzér (SOÓ, 1938); MATRICUM: **N. H.**: Börzsöny-Gebirge: Csóványos-Gipfel (JÁVORKA), Bükk-Gebirge: Hámor (BUDAI, 1906); Lillafüred (KISS, 1911); Mátra-Gebirge: Kékes-Gipfel (JÁVORKA—V. CSAPODY), Mátraháza (GYÖRFFY); Berg Karancs: Somoskő (BÁNYAI, 1970); BAKONYICUM: **WRO. H.** Budapest (KOVÁTS, 1837); **U. H.**: Svábhegy (Schwabenberg) bei Budapest (ENTZ, 1866); Hárshegy bei Budapest (TUZSON, 1906); Hűvösvölgy (BORZA, 1910); Höhe Csillebérc i. d. Ofner Bergen (ANDREÁNSZKY—Z. KÁRPÁTI, 1934); **D. H.**: Pápakovácsi (POLGÁR, 1928); Pilis (1864); **U. H.**: Szentgál (SZEPESFALVY, 1927); Bakonybél (TUZSON—ANDREÁNSZKY, 1920); **N. H.**: Balatonarács (MÁGÓCSY-DIETZ, 1912); Iszkaszentgyörgy (MOESZ et JÁVORKA, 1923); Nadap (TAUSCHER, 1870); Lábatlan (FELFÖLDY, 1953); Nagykovácsi (TAUSCHER, 1870); Urkút (RICHTER);

EUPANNONICUM: **D. H.**: Nyíregyháza (SOÓ, 1933); Debrecen (HAZSLINSZKY, MÁTHÉ, 1933); Doboz (ERDŐS, **KE. H.**); Újkígyós (ERDŐS, 1968, **KE. H.**).

PRAEILLYRICUM: Szársomlyó (HORN, 1936); (KELEMEN—TERPÓ, 1969).

In der Tschechoslowakei (Mähren u. die Slowakei) **WRO. H.:** Vsetin (J. ULEHLA); **N. H,:** Těšin: Końska (PAX, 1885); Brno: Mokrá (F. ŠVESTKA, 1927); Bilé Karpaty (Weisse Karpaten): Skalica (= Szakolca) (E. ŠILLINGEROVA, 1904, P. ŠILLINGER, 1927, **PRU. H.**); **PRU. H.:** Theben = Děvin (= Dévény): Klentice (T. MALINEC, 1933); Devinská Kobyla (= Dévényújfalu) (I. KLÁŠTERSKY et M. DEYL, 1935); **N. H., D. H.:** Trenčin (= Trencsén): (PAX, 1902, ANDRASOVSZKY, 1942); Pressburg = Bratislava (= Pozsony) (BÄUMLER); (Liptovské Hole Liptauer Tatra, = Liptói havasok): Kozi vrch (FREYN); **N. H.:** Zem. Podhradie (= Nemespodhrágy) (HOLUBY); Trentschiner Komitat: Bosác (HOLUBY); Maninschlucht (PAX, N° 23 760); Fatragebirge: Staňkov (= Sztankova) (PAX, 1911); Nitra (= Nyitra): Zobor (PAX, 1909; M. DEYL, 1935, **PRU. H.**); Beskiden: Bobrek (B. GUSTAWICZ, 1878); **PRU. H.** Devin (= Dévény-Theben): Klentice (T. MATINEC, 1933); — Das nordmährische Vorkommen ist auch durch die Zeichnungen von HRUBY (l. c. p. 160, Fig. VI, 1—5) belegt.

In der Ukraine

Transkarpatien (»Karpatorussland«) Komitat. Bereg: Zányka (MARGITTAI, 1926); Podolien: Borschtschow, Zbrutsch (J. WALAS, 165 887, **J. H.**); Dnester: Kościelniki (N° 165 889, 1879).

In Polen

J. H. Ojców (S. KOZŁOWSKI), Beskiden: Duklapass (E. BARADZIEJ—A. FREY—K. LUCHBER).

In Österreich

WRO. H. Wien (KOVÁTS, 1837); Wien (J. BAYER, 1852).

In Jugoslawien: Banat:

U. H.: Deliblát (MÁGÓCSY-DIETZ, 1913); Donautal: **N. H.:** Banat (PAX, 1898); Werschetz = Versec = Vršac (WAGNER; BERNÁTSKY, 1904).

In Rumänien: Siebenbürgen, Banat:

N. H.: Kronstadt = Braşov = Brassó: Pap kútja (MOESZ, 1904); Nadab (Arad) (THAISZ, 1905); Broos = Szászváros = Orăstie (JÁVORKA, 1902), Maramureş — Máramaros (L. VÁGNER); Grosswardein = Oradea = Nagyvárad (SIMKOVICS, 1880); Maramures = Máramaros: Bistra = Bisztra (COMAN, 1942); Klausenburg = Cluj = Kolozsvár (FREYN, 1872); **U. H.:** Südkarpaten: Balta (POLGÁR, N° 145 588); Gross-Schlatten = Obrud = Abrudbánya: Somoskő (J. BÁNYAI, 1910) **N. H.:** Rodna = Radna (CZETZ, N° 23 768); Domugled = Damogled (PAX, 1912).

b. subsp. **gracile** (Unverricht) Terpó stat. et comb. nov.

Syn.: *A. gracile* UNVERRICHT, in Bielz Verh. Sieb. Ver. 5 p. 173 (1854); Fuss, Fl. Tr. p 615 (1866) — *A. intermedium* Schur ex Schott 1860:91, p. p. non Schur, Enum. p. 636; *A. mac.* var. *angustatum* subvar. *gracile* Engl. (l. c.) p. p.

Tuber rotundatum vel discoideum. Scapus foliorum aequans vel superans, spatha flavidoalba tantum tubus intus purpurea; appendix spadius longe stipitata, sursum subito incrassata.

UNVERRICHT bezeichnet als Standort Siebenbürgen (Transsylvanien): Zsep bei Déva = Deva an der Mieresch (Maros = Mureş).

Verbreitung: **WRO. H.:** Mănărade = Monora (J. BARTH, 1874) — dieses Exemplar hat übrigens auch ENGLER gesehen und wie folgt bestimmt: *Arum maculatum* L. var. *β angustatum* ENGL. subvar. *gracile* (UNVER.) ENGL.; — Ganţiu = Gánts (HAYNALD, 1854; ursprünglich als *A. gracile* bestimmt; CZETZ); **D. H.** Komitat Bihar: Săcuieni = Székelyhid (MÁTHÉ, 1931); **N. H.:** Aiud = Nagyenyed (CSATÓ, 1875, N° 23 778; Komitat. Bihar: Szt. Márton (FREYN); Bihar-Gebirge: Remeţ = Remec (A. GULYÁS, N° 23 794); Rodnaer Alpen (A. CZETZ). (CZETZ hat von den bei Gánts gesammelten Pflanzen 30 wurzeltragende Exemplare SCHOTT übermittelt, der diesen *Arum*- Typ *A. transsilvanicum* benannt haben soll (s. das Herbarblatt N° 3773. **N. H.**))

c. subsp. **danicum** (Prime) Terpó stat. nov.

Syn.: *A. mac.* subsp. *danicum* Prime, Watsonia 5. 107—108 (1961)

Die Spatha ist weisslichgrün, durchschnittlich 8,2—18,0 cm lang; die Spadix viel kürzer als die halbe Spathalänge; die Keule im Durchschnitt 15 cm lang. Längenverhältnis Spatha/Spadix beträgt 1 : 2,3 (PRIME, 1961), in extre-

Abb. 18. Arum alpinum subsp. *gracile* (UNVER.) TERPÓ, Aiud=Nagyenyed, i. w. Teil v. Siebenbürgen (Rumänien), leg. CSATÓ

men Fällen 1 : 3,2 (für letzteres ein Beleg aus Apenrade, Schleswig-Holstein, leg. PRAHL **HAU. H.**)

Beschreibung der Unterart nach PRIME:

Surculus maximus cormi in medio situs; folia immaculata et pro longitudine latiora quam in subsp. *maculato*, minus hastata; spatha ad imam partem collata, brevior quam in subsp. *maculato*; spadix cylindrica, non latior basim versus. Chromosomata 2n = 28.

Holotypus: Grönnese Skow, nr. Frederiksvoerk, North Zeeland, T. W. BÖCHER, 11. May 1961, in Herb. København.

Isotypus in Herb. Mus. Brit.

Distributio: Solum in Dania meridionali-orientali.

IV. **Arum ×Soói** Terpó hybr. nov.

(*A. alpinum* × *A. maculatum*)

Tuber plerumque late-ovatum vel subglobosum rarius breve cylindroideum. Lamina fol. hastata vel hastato-sagittata, immaculata rarius maculata. Pedunculus (16,0—32,0 cm longus) petiolo brevior (petiolus 17,0—38,0 cm longus). Spatha lanceolata 10,0—19,0 cm longa, pallide virescens spathae tubus intus in fundo albidus a medio apicem versus angusta zona purpurea notatus. Spadix 4,0—7,0 cm longus, mediam laminam non attingens; clava 1,0—2,0 cm longa, sordide lutea vel pallide violacea oblongula vel cylindroidea, a basi sensim attenuata, obtusata, plerumque stipite duplo longiore, rarius aequante; stamina violacea vel lutea. Dedicavi in honorem acad. R. Soó.

Holotypus: HUNGARIA occ. Mosonmagyaróvár—Halászi 12. V. 1962. leg. CZIMBER—ERDŐS—TERPÓ (N° 18 195). **KE. H.** Fig. 19.
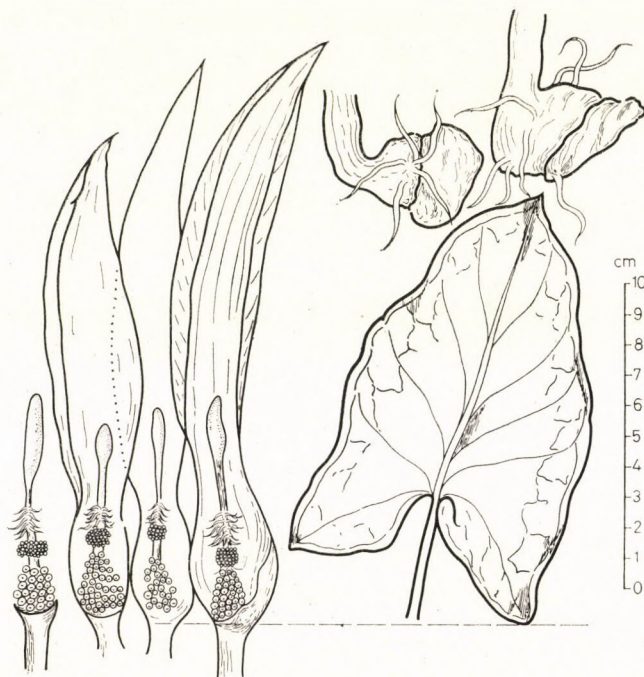
Abb. 19. Arum ×Soói TERPÓ hyb. nov., aus der Gegend von Mosonmagyaróvár (Westungarn)

Auf dem Areal der beiden Elterarten bzw. dem gemeinsamen Verbreitungsgebiet der zwei Arten kommt dieser Typ auch in der Umgebung von Mosonmagyaróvár im Lóvárer Wald (N° 15 541) und entlang der Leitha (N° 15 438) vor. Im Zuge der Bearbeitung des Materials machte ich die Wahrnehmung, dass bei den Hybriden nicht alle Organe gleich sind bzw. dass die Abmessungen zwischen jenen der elterlichen liegen. So z. B. haben die Hybriden eine kürzere Spadix als die Eltern. Die Entwicklungsstufe des blütentragenden Organs dürfte mit der Sterilität der Hybriden zusammenhängen. Auch die Knollen und die Schaftlänge nehmen eine gewisse Mittelstellung ein. Die Staubgefässe können violett oder gelblich gefärbt sein; im Inneren des Tubus sieht man einen zart gefärbten und schmalen purpurroten Streifen.

V. *Arum besserianum* Schott (Österr. Bot. Zschr. 8. 1858: 349); ZAPAL., Conspec. Fl. Galic. I. 248; VISJULINA, Journ. (Žurn.) Inst. Bot. AN URSR 8 (16) 1936: 37; VISJULINA in Flora URSR III. 1950: 9—14; SZAFER, Spraw. Kom. Fiziogr. 48, 1914: 72.

Syn.: *A. maculatum* L. B. I. *Besserianum* (Schott) Aschers. et Graebn. 1904: 376 p. p.; *A. maculatum* L. apud Kuzeneva in Flora SSSR III. p. 487 p. p. — Icon.: VISJULINA, in Journ. Inst. Bot. (l. c.) Fig. 1; SZAFER (l. c.)

Die Knollen sind abgeflacht, rundlich, scheibenförmig, schief- oder horizontalliegend; äusserlich dunkelbraun oder dunkelgrau. Die Blätter sind spiessförmig (hastata), etwas abgestumpft oder spitz zulaufend. Länge der
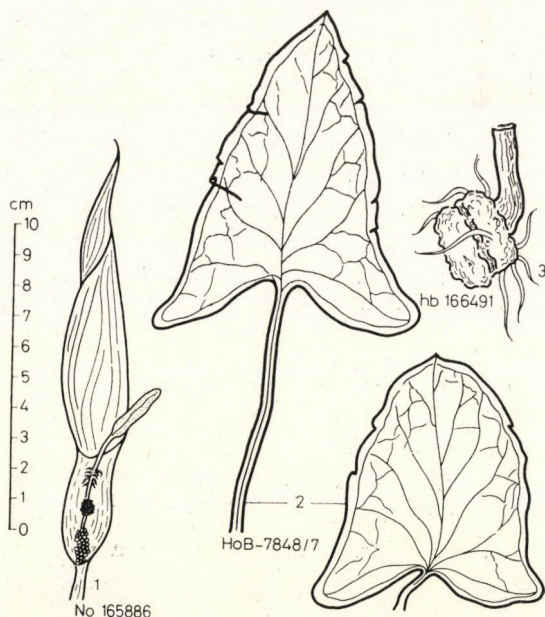
Abb. 20. Arum Besserianum SCHOTT, J. H.: *1*, N° 165 886, *2*, N° B-7848/7, *3*, No 166 491

Blattscheide 8,0—14,0 cm, die des Mittelnervs durchschnittlich 6,0—12,0 (14,5) cm; die Hauptnerven der Basislappen sind 2,5—6,0 (7,0) cm lang. Der Blattstiel (16,0—32,0 cm) ist länger als der Schaft, dieser selbst misst 12,0—20,0 cm. Die Spatha ist 8,0—15,0 (17,0) cm lang, grünlichweiss, seltener bräunlich, die Tubusmitte weiss. Die Spadix ist im Durchschnitt 4,0—7,0 (8,4) cm lang. Die Keule ist zylindrisch oder oblongovoid, abgestumpft, durchschnittlich 1,5—3,0 cm lang; der Stiel (stipes) hebt sich deutlich ab. Die Staminodial-
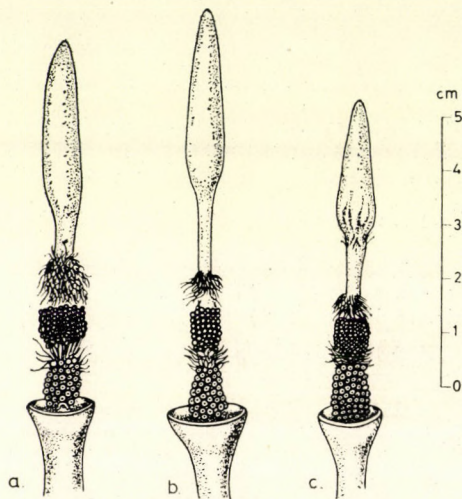
Abb. 21. Arum besserianum SCHOTT, aus der Arbeit von SZAFER (1914), Fundorte in Podolien: a, Czortków, b, Borki Wielkie, c, Kręciłów

blüten entwickeln sich oberhalb der weiblichen Blüten in 2—3, über den Staubblüten in 4 Kreisen. Die Staminodien selbst haben hier keine direkte Verbindung mit den Staubblättern.

Areal (auf Grund der Bearbeitung des **J. H.**): 1. in den südlichen und südöstlichen Teilen Polens, z. B. Ojców nördlich von Krakau, S. KOZŁOWSKI N° B/7847/7; F. BERDAN N° B/7848/8; 2. im Süden u. Südosten des europäischen Teiles der Sowjetunion auf dem Podolischen Rücken, an der Zbrutsch: Miodobory, W. SZAFER N° 166 493, 165 888, 165 890, 165 892; 3. in Gegenden am Dnestr: N° 166 489; WISJULINA (l. c.) berichtet über Vorkommen auch aus der Gegend von Tarnopol, Kamenez-Podolsk, Vinniza.

SZAFER (1914) beschrieb von der Umgebung Miodobory am Zbrutsch eine Varietät, die man als Form für sich bewerten könnte: f. **miodoborense** (Szafer) Terpó comb. nov. (Syn.: *A. b.* var. *miodoborense* Szafer, Spraw. Kom. fizjogr. **48,** 1914: 72). Die Staminodien ober den männlichen Blüten sitzen hier in zwei getrennten Ringen.

Die meisten Autoren hielten diese Art — gestützt auf ENGLER (l. c.) — für *A. maculatum* bzw. für die var. *angustatum*, andere für eine Form *A. orientale*. Ausser der unzulänglichen systematischen Bearbeitung der Pflanze ist an dieser Ungewissheit hauptsächlich auch die ursprüngliche sehr lückenhafte

Abb. 22. Habitusbild von *A. besserianum* (Podolien), aus dem Herbar der Krakauer Jagello-Universität

Beschreibung schuld. Das Taxon *A. besserianum* haben die meisten Verfasser überhaupt nie zu sehen bekommen (z. B. ENGLER 1920: 92), folglich konnte auch das Wissen um diese Pflanze keine Fortschritte machen. SZAFER behauptet, dass die in Podolien heimischen Aronstäbe eher dem Formenkreis *A. Besserianum* angehören. Nach Auffassung dies Verfassers kommt zwar diese

Art in gewissen Formen sowohl dem *A. orientale* als auch dem *A. maculatum* (s. l.) näher, trotzdem hält er sie eher für eine selbständige Art.

VI. *A. orientale* M. B. Fl. taur. cauc. II. 1808: 407, emend. Engler in DC mon. Phan. II. 1879: 587, agg.

Flache, scheibenförmige Knolle, am Grunde spiess- bzw. pfeilförmige Blätter. Der Schaft kann kürzer oder länger als der Blattstiel sein, aber auch

Abb. 23. Arum orientale, aus der Monographie Hrubys (1912: 147) (Herbarium Jurjews). Gegend von Dnepropetrovsk (vorm. Jekaterinoslaw; Steppenzone)

genauso lang. Die Spatha ist 10,0—26,0 cm lang und intensiv oder bräunlich purpurfarben, das Anhängsel ebenfalls purpurn; die Keule ist gewöhnlich 2,0—10,0 cm lang, zylindrisch. Die unteren und oberen Staminodien (2) bestehen aus 3 bis 4 Kreisen und sind von den Staubblüten klar spationiert.

Aus *A. orientale* machte Engler (l. c.78) eine grosse Sammelart. Vergleicht man das Englersche System mit den wertvollen Untersuchungen Wulffs (1926: 46—49), lässt sich feststellen, dass im osteuropäischen Raum das Vorhandensein dreier Formenkreise (*elongatum*, *orientale* und *albispathum*) von *A. orientale* anerkannt bzw. am häufigsten publiziert wird.

Nach den einzelnen Autoren (Wulff, l. c. Kuzenewa, 1935: 485) soll *A. orientale* auch in den Nord-, Ost- u. Südkarpaten bzw. in Mitteleuropa vorkommen. Neuerdings meldet dieses Taxon Dihoru (1970) als häufige Pflanze aus Rumänien (z. B. aus der Umgebung von Bukarest). Ausserdem kommt sie

noch (Kusmanov, 1964: 139) auf dem Balkan, in der Krim (**U. H.**: Sammlung von Soó aus 1959!), in der Südukraine, im Kaukasus, in Kleinasien und im Iran vor; Dihoru (l. c. p. 83) hat im ungarischen Bükk-Gebirge eine Abart *A. alpinum* var. *intermedium* gesammelt.
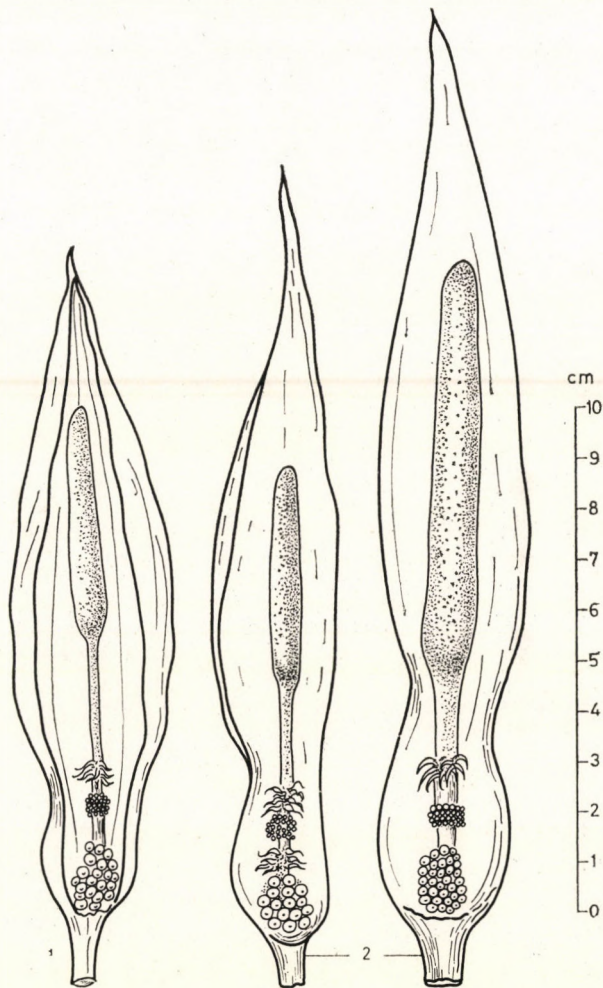
Abb. 24. 1, 2 *Arum orientale* M. B.; 1) nach dem Herbarexemplar Soós, 2) nach Herbarexemplaren des Herbars d. Univ. Wrocław

Es lässt sich feststellen, dass im ganzen uns zugänglichen *Arum*-Schrifttum vor allem die Bearbeitungen von Engler (l. c.) und Wulff (l. c.) sichere Grundlagen für die weitere Forschung liefern. Wir wollen deshalb im weiteren die in Osteuropa und auf dem Balkan vorkommenden, das Gebiet des Karpatenbeckens berührenden und von hier angegebenen »Kleinrassen«, »Abarten«

A. orientale dieses noch äusserst wenig untersuchten Komplexes auf die genannten zwei Verfasser aufbauend behandeln.

a. *A. orientale* M. B. (s. str.) Fl. taur. cauc. II. 1808: 406, Wulff (l. c.); *A. orientale* ssp. *euorientale* var. *typicum* Engl. (l. c.) Fig. 12. c. Horizontale Rhizomstellung, scheibenförmige Knolle. Blattspreite breit und kurz, von 7,0—8,2 cm Länge; Basislappen 2,5—4,5 cm lang. Der Blattstiel ist in der Regel viel länger als der Schaft, manchmal aber gleichlang. Die Spatha ist eiförmig oder elliptisch, 8,0 bis 13,0 cm lang, die Spadix länger als die halbe Spatha. Die Keule misst durchschnittlich 1,6—4,5 cm in der Länge und 0,3—0,5 cm in der Stärke; der Keulenstiel ist äusserst kurz.

Verbreitungsgebiet: Mittellauf des Dnepr, Küstengebiete des Schwarzen Meeres, die Krim (Herkunftsland des Holotyps), Balkanhalbinsel, Kleinasien usw.

b. *A. elongatum* Stev. in Bull. Soc. Natur. Mosc. XXIX. 1856: 265, 1857: 67, No 1337.

Syn.: *A. orientale* M. B. v. *elongatum* Boissier V. 1867: 39. *A. orientale* M. B. ssp. *elongatum* (Stev.) Engl. var. *Stevenii* Engl. (l. c. 79) Fig. 12 E.

Knolle wie bei *A. orientale.* Die Blattspreite ist länglich, sie misst 10,0—20,0 cm in der Länge, die Basislappen sind 5,0—9,0 cm lang. Der Schaft ist wesentlich länger als der Blattstiel. Die Spatha ist lanzettlich, länglich zugespitzt, mitunter bis zu einer Länge von 26,0 cm, von aussen weisslich. grünlich, von innen bräunlichpurpurfarben. Die Keule ist 4,5—10,0 cm lang, violett oder purpur, mit einem sehr kurzen Stiel.

Verbreitungsareal: Schwarzmeerküste, Krim, Balkan, Kleinasien usw. Beschrieben aus der Umgebung von Simferopol.

Zusammenfassung der biometrischen Untersuchungen

Mein besonderes Anliegen war es, die Beziehungen zwischen den Formenkreisen durch zahlenmässige Charakterisierung der Eigenschaften der pflanzlichen Organe konkret darzustellen. Von den angeführten Taxa hat die biometrischen Daten von *A. maculatum* subsp. *danicum* Prime (1955) tabellarisch verarbeitet. Diese Daten vergleicht dann Riedl (1967) mit seinen eigenen statistischen Auswertungen.

Im Zuge der weiteren Untersuchungen kamen wir zu der Erkenntnis, dass ausser der numerisch-quantitativen Auswertung — die sehr brauchbare Angaben lieferte — auch gewisse morphologische Eigenschaften gute Merkmale, sichere Unterlagen darstellen. So u. a. die Form der Knolle, des Blattes, der Keule, die Färbung der Antheren, des Tubusinneren, der Spatha, die Geflecktheit oder Ungeflecktheit des Blattes (s. S. 217).

Im Sinne des Gesagten trachtete ich jedenfalls auch Merkmale herauszuheben und auszuwerten, die nicht nur eine minüziöse taxonomische Unter-

teilung der Art gestatten, sondern beim Sammeln oder im Herbar eine raschere Bestimmung der Pflanzen ermöglichen.

a) Frucht und Samenzahl

Im Laufe der Entwicklung der Individuen von *A. maculatum* und *A. alpinum* gibt es zwei Perioden, in welchen man die Pflanzen auch in situ, ohne sie auszugraben, unterscheiden kann: während der Blütezeit und während des Reifens der Frucht. Die hier folgenden Angaben lassen darauf schliessen, dass zur Unterscheidung der Arten auch die Kennzeichen der Früchte herangezogen werden können. Die Früchte von *A. alpinum* sind länglich, eiförmig, die
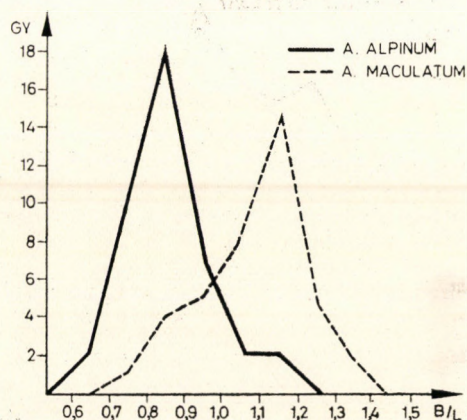
Abb. 25. Verhältnis Fruchtbreite/Fruchtlänge bei *Arum alpinum* und *A. maculatum*

von *A. maculatum* an den Enden abgekappt, so dass sie — wie aus der beigegebenen Aufstellung ersichtlich — breiter sind als lang.

Die Unterschiede der beiden Arten werden auch durch die graphische Darstellung der Häufigkeitswerte (Breite/Länge) gut veranschaulicht. Zwischen den Früchten der beiden Arten ergaben sich je nach Standorten nur ganz geringfügige Abweichungen.

Auch die Zahl der in einer Frucht enthaltenen Samen war Gegenstand von Untersuchungen (PRIME l. c.). Weiter unten finden sich Häufigkeitswerte der vollentwickelten Fruchtensamenzahl bei *A. alpinum* und *A. maculatum* von verschiedenen Standorten (Abb. 27). In dieser Eigenschaft der beiden Ar-

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A. alpinum (im Bakony-Gebirge): (Csatka-Koromla) 1 : 0,85
A. alpinum (im Vértes-Gebirge: Vérteskéthely) 1 : 0,86
A. maculatum (im Mecsek-Gebirge) 1 : 1,04, 1 : 1,08 (Dessau: a. d. Elbe) 1 : 1,12

Durchschnittliche Verhältniswerte Fruchtbreite/Fruchtlänge.
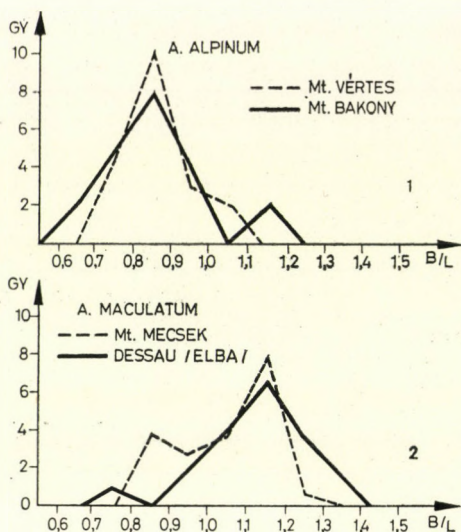
Abb. 26. 1) Vergleich der Verhältniswerte Fruchtbreite/Fruchtlänge bei *A. alpinum*-Belegen von zwei Standorten (Vértes- u. Bakony-Gebirge, Hung. bor.-centr.), 2) Vergleich der Fruchtdaten von *A. maculatum* zweier Standorte, u. zw. vom Lauf der Elbe (Dessau) und aus Südtransdanubien in Ungarn (Mecsek-Gebirge)
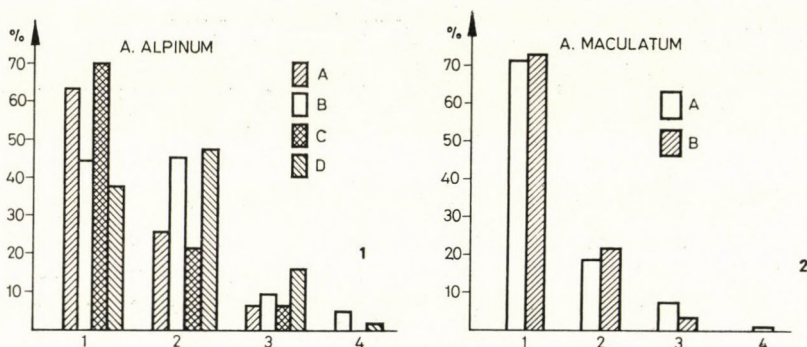
Abb. 27. Samenzahl je Fruchtbeere (prozentuale Häufigkeit) bei *A. alpinum* und *A. maculatum* von verschiedenen Standorten:

1) *A. alpinum*		2) *A. maculatum*	
A — Vitnyéd	Hung. occ.	A — Répcelak	Hung. bor. occ.
B — Nagygeresd		B — Halászi	
C — Csatka	Hung. centr.		
D — Dunasziget	Hung. bor. occ.		

ten besteht ein wesentlicher Unterschied insofern, als bei *A. alpinum* ganz auffallend häufiger zweisamige Beeren vorkommen, aber auch Beeren mit drei Samenkernen relativ häufig anzutreffen sind.

Tabelle 1

Länge in mm		*Arum italicum*	*Arum maculatum*			*Arum alpinum*				*A. besserianum*	*A. orientale*
		Durchschnitt	Herbarien	Eigene Sammlung 1968–1970	Durchschnitt	Herbarien	Belege aus Polen J. H.	Eigene Sammlung 1968–1970	Durchschnitt	J. H. Krakau	Herbarien
Mittelnerv	*M*	114,90	103,75	103,59	103,67	90,38	83,16	88,04	88,81	96,40	115,80
Blattseitennerv	*VL*	*67,08*	*53,92*	*53,11*	*53,54*	43,58	44,10	45,48	44,50	46,80	54,86
Blattstiel	*PE*	275,06	247,87	276,54	263,43	253,89	299,30	280,31	269,30	243,60	242,06
Schaft	*SC*	135,90	157,56	181,58	167,82	*251,48*	*294,00*	*260,46*	258,22	158,90	131,30
Spatha	*SP*	200,70	189,97	135,76	169,27	*116,20*	*123,30*	*102,97*	*111,62*	120,80	121,80
Spadix	*I*	84,57	78,64	59,00	71,37	62,63	62,00	57,12	60,56	57,30	92,66
Keule	*C*	—	—	14,75	14,75	—	14,3	*12,90*	13,13	18,30	45,40

Tabelle 2

I. Längenverhältnisse		*Arum italicum*	*Arum maculatum*			*Arum alpinum*				*A. besserianum*	*A. orientale*
		Durchschnitt	Herbarien	Eigene Sammlung 1968–1970	Durchschnitt	Herbarien	Belege aus Polen J. H.	Eigene Sammlung 1968–1970	Durchschnitt	J. H. Krakau	Herbarien
Blattseitennerv/Mittelnerv	*VL/M*	0,58	0,58	0,51	0,54	0,49	0,48	0,52	0,50	0,48	0,46
Schaft/Blattstiel	*SC/PE*	0,47	0,63	0,66	0,64	*0,99*	*0,96*	*0,94*	*0,97*	0,64	0,45
Spadix/Spatha	*I/SP*	0,42	0,45	0,44	0,46	0,54	0,49	0,56	*0,54*	0,47	*0,74*
Keule/Blütenstand	*C/I*	—	—	0,24	0,24	—	0,23	*0,22*	0,22	0,31	0,46
II. Blattstiel/Schaft	*PE/SC*	2,06	2,02	1,54	1,81	1,00	1,04	1,07	1,03	1,61	1,84
Spatha/Blütenstand	*SP/I*	2,38	2,41	2,25	2,36	1,83	2,03	1,54	1,63	2,12	1,31

Bemerkung: Zum Zwecke der Auswertung wurden aus dem Herbarmaterial Belegbögen von folgenden Arten u. in folgender Anzahl gemessen:

A. italicum	25	Herbarbögen	*A. Besserianum*	13	Herbarbögen
A. maculatum	100	Herbarbögen	*A. orientale*	10	Herbarbögen
A. alpinum	200	Herbarbögen			

Die Messwerte der lebenden Pflanzen wollen wir hier nicht mitteilen, da ihr Vergleich mit dem Herbarmaterial die Durchschnittswerte verzerrt hätte. M. E. sind auch die Clava-Angaben des älteren Herbarmaterials infolge der Eintrockung als geringer anzusehen.

b) *Laubblätter und Blütenstand*

Das Verhältnis zwischen Spatha- und Spadix-Länge haben auch schon PRIME (1955) und RIEDL (1967: 163) untersucht. Die Gelegenheit hierzu bot beiden Verfassern vor allem die Beschreibung bzw. Kritik des Taxons *A. maculatum* subsp. *danicum*. Nach PRIME (l. c.) beträgt die Spathalänge der Subspecies *danicum* 8,2—18,0 cm, während sich die Länge der Spatha zu jener der Spadix wie 1 : 2,3 verhält. Bei der ssp. *maculatum* verhalten sich diese Längen wie 1 : 3,3.

RIEDL (l. c.: 163) ging auf Grund von 10 niederösterreichischen Herbarbelegen (**HW**) von *Arum* die Durchschnittslänge der Spatha mit 10—12 cm, die der Spadix mit 5,5—7,0 cm an; als durchschnittliches Verhältnis ihrer Längen zueinander hat er 1 : 1,8—1,9 gefunden. Der Verfasser meint, der in Wien (**HW**) aufbewahrte Isotypus der subsp. *danicum* zeige kaum greifbare Unterschiede im Vergleich zu den Belegexemplaren der Form *immaculatum*. Seine Meinung findet er auch dadurch bestätigt, dass einige Autoren gerade bei *immaculatum* Rchb. 2n = 28 Chromosomen gezählt haben. Wie aus den hier folgenden Tabellen hervorgeht, entsprechen hier die Werte von *A. alpinum* den Messdaten RIEDLs, u. zw. sowohl für die Durchschnittswerte als auch für die Verhältniszahlen (Tab. 2, II).

Wenn man die Daten für die in Tabelle 1, verzeichneten Arten miteinander vergleicht, kann man gleich auch auf abweichende Blattformen schliessen. So sind z. B. die Blattseitennerven bei *A. maculatum* und *A. orientale* länger, weil die Basislappen seitlich stärker abstehen. Bei *A. Alpinum* ist der Schaft auffallend lang, doch findet sich hier auch die kürzeste Spatha; ähnlich gibt es hier auch die kürzeste Clava — im Gegensatz zur 5 cm langen Keule von *A. orientale*, die selbst 10 cm lang werden.

An gleiche Erscheinungen erinnern aber auch die Längenverhältnisse. Das in den Bestimmungsschlüsseln immer wieder erwähnte Verhältnis Basislappe/Mittelnerv ist bei *A. orientale* das kleinste (1 : 0,46), um dann sukzessive die halbe Länge von Basislappen und Mittelnerv zu übersteigen. Die Spadix hingegen ist vor allem bei *A. orientale*, in geringerem Masse bei *A. alpinum* länger als die halbe Spatha. Lediglich zur Information möchte ich hierzu erwähnen, wie weit die infraspezifischen Populationen voneinander abweichen können. Im *alpinum*-Material besitzen z. B. die kürzeste Spatha (mit durchschnittlich 92 mm) und — im einheimischen Material — den längsten Schaft (284 mm) die Belege aus Tatabánya (Vértes-Gebirge) (SP/SC = 1 : 0,32). Die Proportion der Länge des Spatha zu jener des Schaftes aber ist im grossen und ganzen dennoch gleich eins (1 : 1,09).

Auch die Auswertung der hier folgenden graphischen Darstellung lässt bestimmte Verwandtschaftsbeziehungen vermuten, die im Verlauf der Kurven gut zum Ausdruck kommen. Es lassen sich nämlich zwei im wesentlichen ähnliche Kennlinien unterscheiden, u. zw. auf Grund der Gruppierungen 1. *alpi-*
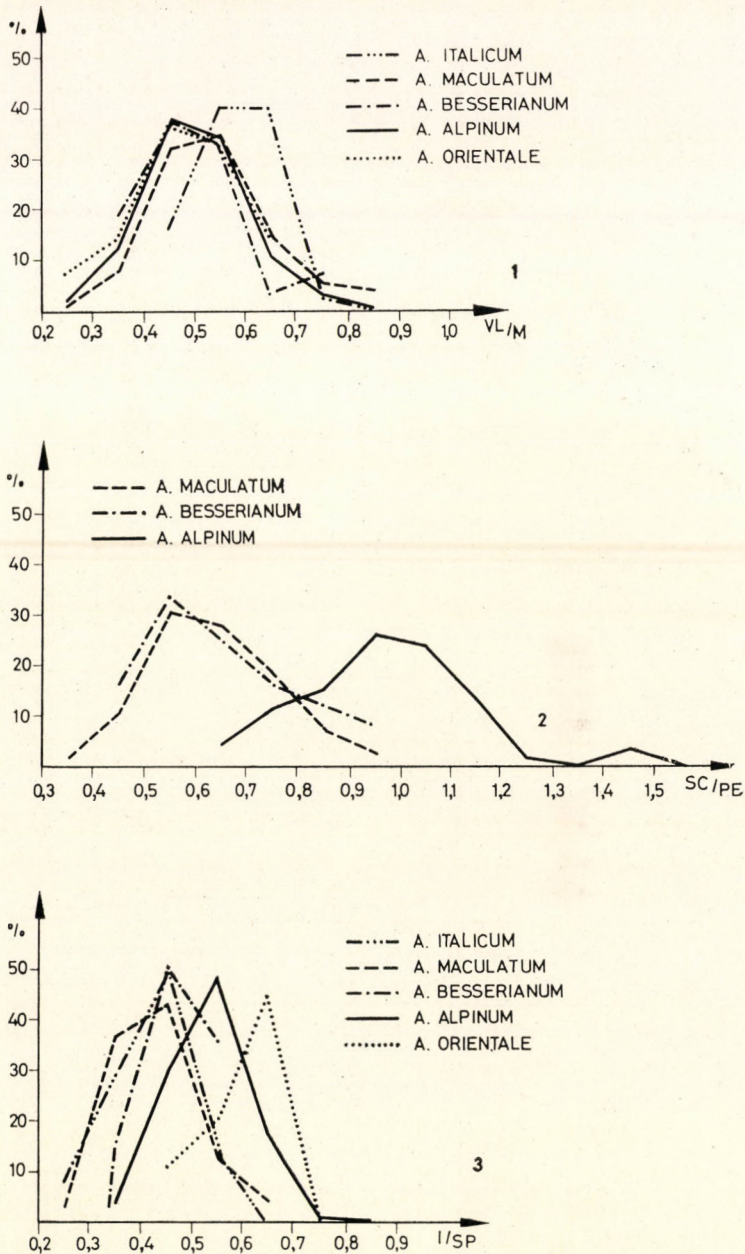
Abb. 28. Die Zahlenwerte der Blütenstände und der vegetativen Teile in graphischer Darstellung (als Häufigkeitsdiagramme):

$$1)\ \mathrm{VL/M} - \frac{\text{Blattseitennerv L.}}{\text{Mittelnerv L.}}, \qquad 2)\ \mathrm{SC/PE} - \frac{\text{Schaft L.}}{\text{Blattstiel L.}},$$

$$3)\ \mathrm{I/SP} - \frac{\text{Blütenstand L.}}{\text{Spatha L.}}$$

num, *besserianum* und *orientale* sowie 2. *italicum-maculatum*. Auf dem Diagramm I/SP stehen auf der linken Seite jene Arten (*italicum*, *maculatum*, *besserianum*), deren Spadix kaum die halbe Länge (wenn nicht weniger) der Spatha erreicht. Die verhältnismässig längste Spadix hat die von dieser Gruppe abgesetzte, zuäusserst stehende *A. orientale*.
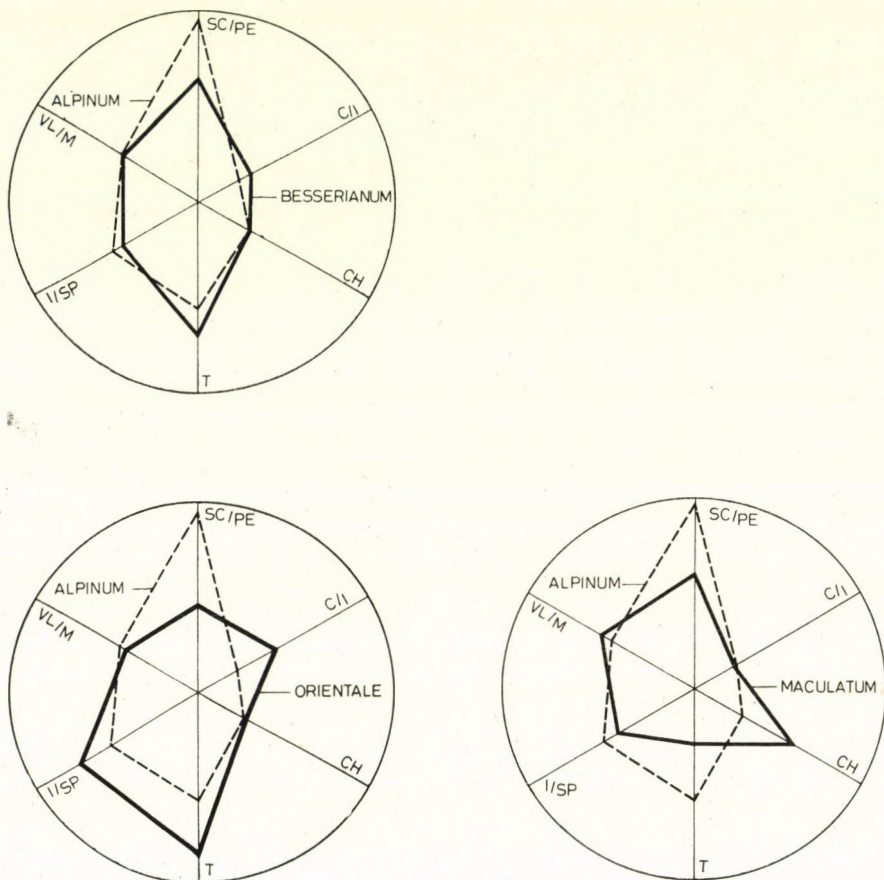
Abb. 29. Die Verhältnisse der Eigenschaftspaare sowie die Chromosomenzahlen und die Kennwerte der Knollenformen, in polygonalem Diagramm

Zur Veranschaulichung der verwandtschaftlichen Zusammenhänge habe ich schliesslich noch ein polygonales Diagramm konstruiert, in welchem die Quotienten der Eigenschaftspaare, die Chromosomenzahlen (CH) sowie die Gestalt des einen Merkmales — der Knolle (T) — aufgetragen sind. Die Gegenüberstellung der Knollentypen und der Chromosomenzahlen lieferte folgende Werte:

	Maculatum	Alpinum	Besserianum	Orientale
CH	0,56	0,28	0,28	0,28
T	0,28	0,56	0,70	0,84

Sämtliche Werte sind mit dem Fünffachen ihrer natürlichen Grösse aufgetragen. Die stärksten Abweichungen zeigen sich bei der *alpinum*- bzw. *maculatum*-Kurve, besonders hinsichtlich des Chromosomensatzes und des Quotienten Schaft : Blattstiel.

Abschliessend möchte ich noch für die mir bei den Aufnahmen und Terrainarbeiten geleistete Hilfe meinen besonderen Dank den Assistenten E. Grusz, M. Nagy, E. Pintér und M. Pisák sowie der Oberassistenten Dr. Pomogyi-Terpó (Lehrstuhl f. Pflanzenschutz a.d. Universität f. Gartenbau), ferner für die photographischen Aufnahmen und die Anfertigung der Bilder den Frau E. Horváth und Frau M. Lexa (5 Zeichnungen) sowie für die Mitwirkung bei der Ausführung der Zeichnungen V. Weigel ausdrücken.

Bestimmungsschlüssel der wichtigsten Taxa

1 a Blätter gefleckt, Antheren gelb 2
b Blätter ungefleckt 5

2 a Blätter marmoriert; entlang der Adern mit hellen weisslichen Feldern 3
b Blätter zart schwarzlila gefleckt 4

3 a Auffallend spiessförmige Blätter; die Länge des Basislappens kann bis zu Dreiviertel des Mittelnervs erreichen. Die Pflanze ist hochgewachsen (60 cm), treibt im Herbst abermals. Länge der Spatha: 18,0—0—30,0 cm, Farbe weisslich; Keule gross u. dick, lang zylindrisch geformt, gelb (durchschnittlich 3,0—7,0 cm lang, 0,5—1,0 cm dick). Die Spadix nicht länger als die halbe Spatha. Rhizom zylindrisch, tiefpurpurbraun. Die Art ist typisch für den atlantisch-mittelländischen Raum, 2n=84 (64) Mill.. I. *A. italicum*
b Der Basislappen der Spreite ist kürzer als Dreiviertel der Mittelnervlänge. Die Pflanze selbst ist niedriger, im Herbst treibt es nicht aus. Rhizom elfenbeinfarbig oder gelblichbraun 4

4 a Blätter spiessförmig, lilaschwarz gefleckt oder ungefleckt (var. *immaculatum*), selten mit weisslichen Feldern entlang der Adern, immer spiessförmig, mit offenem oder geschlossenem Blattgrund, wobei die Basislänge in der Regel nur ganz unbeträchtlich länger als der halbe Mittelnerv des Blattes (1 : 0,54), der Schaft ist stets kürzer als der Blattstiel (1 : 0,64); die Spatha ist 12,0—25,0 (30,0) cm lang, grünlichweiss (selten ebenfalls lila gefleckt); die Keule gewöhnlich von mittlerer Grosse, 3,0—7,0 cm lang, lila oder gelblich, in den Stiel verlaufend, die Spadix etwa bis zur halben Spathalänge reichend (1 : 0,46), die Antheren gelb. Atlantisch-submediterrane Art, 2n=56 ....
II. *A. maculatum* L. emend. Mill.
b Die Blätter am Grunde spiess-pfeilförmig, nur spärlich mit ganz kleinen lilaschwarzen Flecken, aber auch ungefleckt. Der Schaft ± kürzer als der Blattstiel (1 : 0,84); Spatha grünlichweiss und 10,0—19,0 cm lang; Spadix 4,0—7,0 cm, kürzer als die halbe Spatha (1 : 0,43); Knollenform gedrungen, kurz-zylindrisch, von bräunlicher Färbung.........
IV. *A.*×*Soói* Terpó

5 a Am Grunde pfeilförmige Blätter, Basisseitennerv so lang wie der halbe Mittelnerv (1 : 0,50), Schaft ± gleich lang wie der Blattstiel; Spatha kurz (8,0—12,0 cm) und grünlich; zart lila umrandet (subsp. *alpinum*) Tubus im Innern purpurfarben, Keule langstielig, sie selbst ist schmal und kurz — 0,7—2,0 cm lang — und spindelförmig; die Spadix zart lila oder schmutzgelb, steht aus der Spatha kaum heraus, ist gewöhnlich länger als die halbe Spatha; die männlichen Blüten sind purpurlila, das Rhizom eiförmig abgeflacht,

aufwärtsstehend, elfenbeinfarben: Autochthon pannonische (mitteleuropäische) Art 2n=28

III. *A. alpinum* Schott et Kotschy emend. Terpó

b Rhizom rundlich, Schaft ± von gleicher Länge wie der Blattstiel; Spatha weisslich oder grünlich, Keule wie bei *A. alpinum* 6

c Schaft kürzer als der Blattstiel, Keule dick, mittellang oder gross, länglich ovoid oder zylindrisch, von ihrem Stiel scharf abgesetzt. Blattspreite spiessförmig 7

6 a Rhizom rundlich oder halbkugelig, seitlich geneigt oder horizontal liegend, elfenbeinfarben, die Spatha grünlich oder zart veilchenblau gerandet, die Keule wie bei *A. a.* var. *pannonicum* .... *A. alpinum* var. *intermedium* (Schur) Terpó

b Spatha weisslich, bis aufs purpurgetönte Tubusinnere, die Keule langgestielt, mit jäher Verdickung der Spitze. Das (oft schrägstehende) Rhizom ist rundlich scheibenförmig. (Rumänien: Siebenbürgen) ....

A. alpinum subsp. *gracile* (Unverricht) Terpó

7 a Spatha 8,0—15,0 (17,0) cm lang, grünlichweiss, seltener bräunlich, Tubus innen weiss, die Keule oblong-ovoid und von mittlerer Grösse (1,5—3,0 cm lang); die Spadix bleibt unter der halben Spathalänge; das Rhizom hat gewöhnlich Schrägstellung und eine rundliche oder scheibenähnliche Form .... V. *A. besserianum* Schott

b Rhizom horizontal gelagert, oben eingetieft, scheibenförmig, die Blattspreite kurz und breit; der Schaft kürzer als der Blattstiel; die Spatha purpurfarben, 8,0—13,0 cm lang; die Spadix länger als die halbe Spatha; die Keule Purpurgetönt, gewöhnlich grösser zylindrisch (2,0—4,5 cm lang), der Stiel sehr kurz. Pontisch-mediterrane Art; 2n=28......

VI. a *A. orientale* M. B. (s.s.)

Rhizom wie oben; Blattspreite länglich, der schaft bedeutend langer als der Blattstiel; überlange Spatha(—26,0 cm); grosse, 4,5—10,0 cm lange purpurfarbene Keule ....

VI. b *A. elongatum* Stev.

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HISTOCHEMICAL AND HISTOAUTORADIOGRAPHIC EXAMINATION OF ALKALOID LOCALIZATION IN THE VEGETATIVE ORGANS OF DATURA INNOXIA MILL.

By

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Alkaloid localization in the vegetative organs of *Datura innoxia* Mill. was investigated-with histochemical methods as well as by histoautoradiography after absorbtion of radioactive atropine.

MAYER, DRAGENDORFF, Hexachloroplatinum, SCHEIBLER and other reagents were used for the histochemical purposes. For the isotopic examinations histoautoradiography was used with emulsion-technique after the absorbtion of generally marked H^3-atropine borate.

It could be inferred that alkaloids are found in crystal form in the separated idioblasts and intercellulars of the pith — and the phloem — parenchyma of plants as well as in their root hairs. Besides, alkaloids also occur in liquid state in the cells of the head of glandular hairs.

The plant takes up the radioactive alkaloid, which is then transported in the xylem and gradually passing towards the inactive excreting areas excretes in the form known from histochemical investigations.

Introduction

The biochemical researches of recent decades have made much progress towards the knowledge of biosynthesis and biogenesis in alkaloids. Isotope technique, along with other sensitive biochemical methods, established the possibility of in vivo research into alkaloids. Much is known now about the formation of certain alkaloids. However, their function in metabolism is still a question of discussion.

The tropane alkaloids, occurring in *Datura* species are owing to their simple traceability, the subject of easier investigations, so many of their metabolic characteristics have already been determined as for example, the fact that in certain plant species as e.g. *Datura ferox* and *D. stramonium* epoxidation of hyosycamine into scopolamine takes place in the epigeal organs (shoots). (Cf. ROMEIKE 1960, 1970, 1971). In other *Datura* species, e.g. *Datura innoxia*, also the root is able to epoxidize, therefore a considerable quantity of scopolamine occurs also in the root (LUCKNER 1969; VERZÁR-PETRI 1964). In the same species vigorous teloidine metabolism can also be demonstrated (VERZÁR-PETRI 1964, LIEBISCH 1966, EVANS 1966). Here the strating compound, 7—OH, 3—6 ditigloil-teloidine, occurs in the root, while the monotigloil-teloidine (= meteloidine) is to a more considerable extent characteristic of the shoot. These data

call attention to the fact that the alkaloid production of the various vegetative organs is different and that the tissues in them have different characteristics as regards producing and localizing the alkaloid.

These biochemical considerations turned my interest towards dealing with the question of alkaloid production and localization by a histological approach. This seemed to be all the more substantial since data on the localization of alkaloids in plant tissues are available mostly from the past century only. Admittedly, cultivation of plant tissue cultures has also been developing recently, for there has been hope of opening up practical industrial aspects on a larger scale. This also has given rise to the importance of production biological evaluation of tissues, as well as to the timeliness of knowing their substance metabolism.

It is only *Datura stramonium* among the *Datura* species concerning which there are data available (JAMES in MANSKE—HOLMES 1950). According to these, alkaloids can be demonstrated in one of the layers of the testa and in the glandular hairs of the foliage leaf. As for my own data, up to now I have dealt with the preparative ultracentrifugalization of *Datura innoxia* and *Vinca minor*, with an aim to determine the alkaloid content of the various cell fractions (VERZÁR-PETRI 1969—1970). In addition to the cytological survey, histochemical and histoautoradiographic examinations were set first with *Vinca minor* studied by me recently (1969, 1970) in detail also from a biochemical point of view. Then, seeing the efficiency of the combined method, I extended my investigations to the alkaloid localization in *Datura innoxia* Mill., by again applying the histochemical and histoautoradiographic combined procedure. The results of these examinations are given below.

Material and method

Datura innoxia seedlings and young shoots were used for the investigations. The plants were grown in the Biological Research Station, of the LORÁND EÖTVÖS University at Alsógöd. Seeds for germination, young shoots as well as roots in certain cases were obtained from grown blossoming plants there.

For histochemical investigations various alkaloid reagents, recommended by TUNMANN—ROSENTHALER (1931) were used as, for example, DRAGENDORFF reagent; WAGNER reagent ($KJ \cdot J_2$); acidic alcoholic alkaloid dissolution (differentiation) after JAMES, used as control and modified on the basis of ERRARA; hexachloroplatinum; picric acid reagents; and last but not least potassium-tetraiodo mercurate (= MAYER reagent) recommended by SZÁSZ (1966) also for analytical purposes, and successfully tried in histochemistry with *Vinca minor* (VERZÁR-PETRI 1970). The reactions were always carried out on fresh material by placing the hand-cut sections directly into the reagent and storing them in general for 24 hours in it. Then great care was taken to wash the sections and to the differentiation mentioned above. The named alkaloid reagents provide precipitates with alkaloids and after suitable washing and differentiation, the areas of localization unambiguously manifest themselves. The tissue areas or cells not containing alkaloids remain entirely unstained.

Along with the alkaloid reagents mentioned above, histoautoradiography was also applied. For this, generally marked H^3-atropine-borate with a specific activity of 1.23 μCi/mg was used; the quantity of material used for incubation was 50 mg/50 ml in distilled water. The shoots to be incubated were merged in this for 1—3 days, while mild air was transfused. Then the samples were taken out of the solution, washed throughly and immediately processed.

Results and discussion

On the basis of the histological and histochemical investigations it may be stated that the various alkaloid reagents produce uniform results. It was only in the colour of reactions and in their intensity where deviation occurred. The most intensive colour reaction was produced by the DRAGENDORFF reagent. The observations made by means of the various reagents were however, in qualitative agreement.
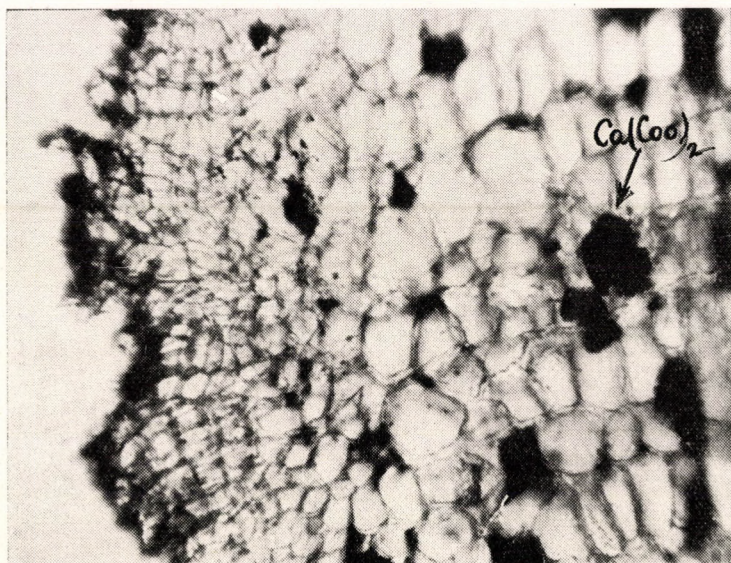
Fig. 1. Formation of calcium-oxalate crystal sand in the dilatation zone of the old root. Magn. = obj. 8 × oc. 5

As regards the unstained and control preparations it was above all noteworthy that various crystals differing from one another in shape and size occur in the tissues of *Datura innoxia*. Among these crystals, only the rosette crystals well known on the foliage leaf, and the sand crystals to be found in idioblasts appearing in the phloem of the stem and root, proved to be calciumoxalate crystals. All the others — occasionally laminate or irregular sphaero-crystal and smaller pyramidal-octahedron crystal combinations, which occur in the company of several others, or lonely, or frequently in pairs in the primary cortex of the root and stem as well as in the extended pith of the stem, mainly in the parenchymatous cells on the border of the intraxilar phloem — produce an alkaloid-positive reaction, and therefore they qualify as alkaloid crystals. They do not respond to the usual calcium and oxalate tests. Figures 1 and 2 show examples of this. The typical alkaloid positive crystals resemble the at-
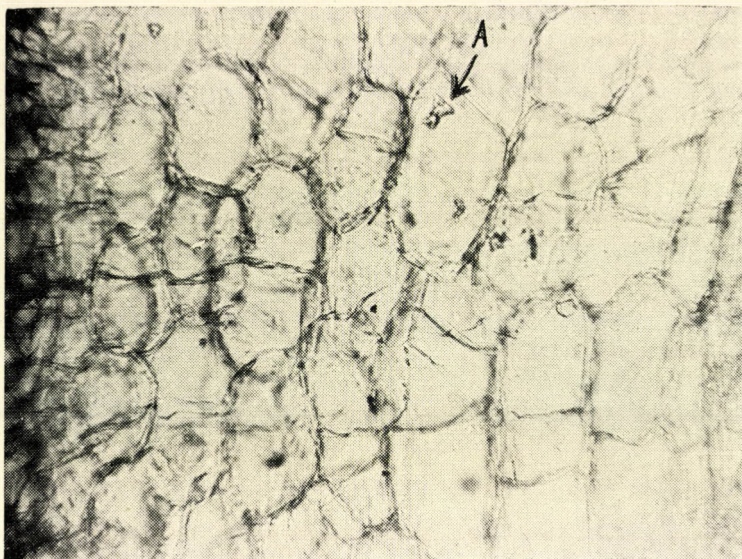
Fig. 2. Same tissue area as in Fig. 1 after treatment with R-HCl. Calcium-oxalate crystals have dissolved, while the alkaloid crystals remained. Magn. = obj. 8× oc. 5
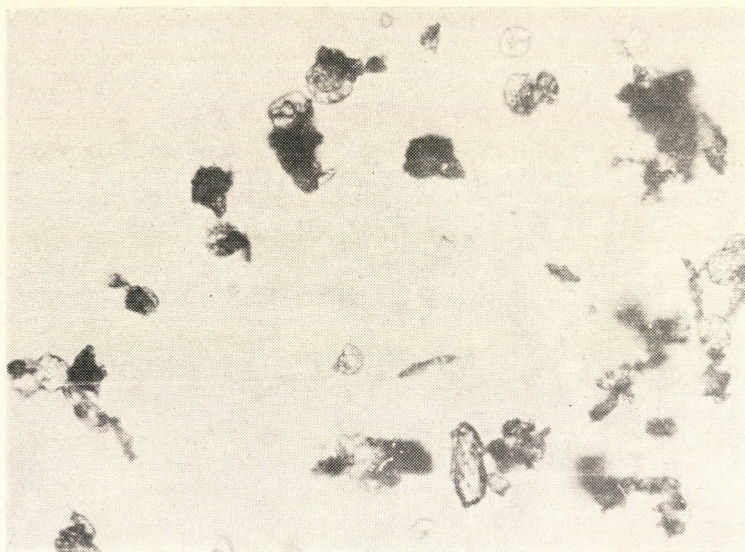
Fig. 3. Optical microscopical picture of standard atropinborate. Magn. = obj. 40 × oc. 5

ropine-borate crystal in shape, observable on standard chemicals (Figs 3, 4 and 5).

The formation of intercellulars both in phloem and pith is characteristic of the parenchymatous tissue of *Datura innoxia*. The intercellulars are only
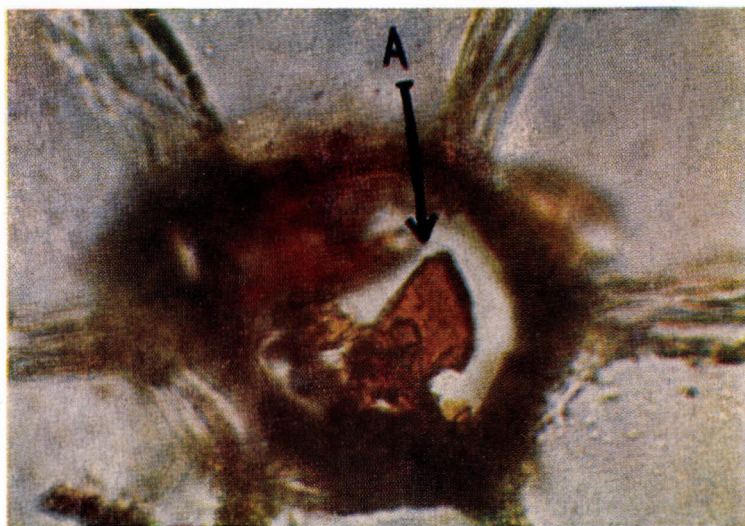
Fig. 4b. Histochemical reaction of alkaloid crystals by DRAGENDORFF reagent. Magn. = obj. 40 × oc. 5
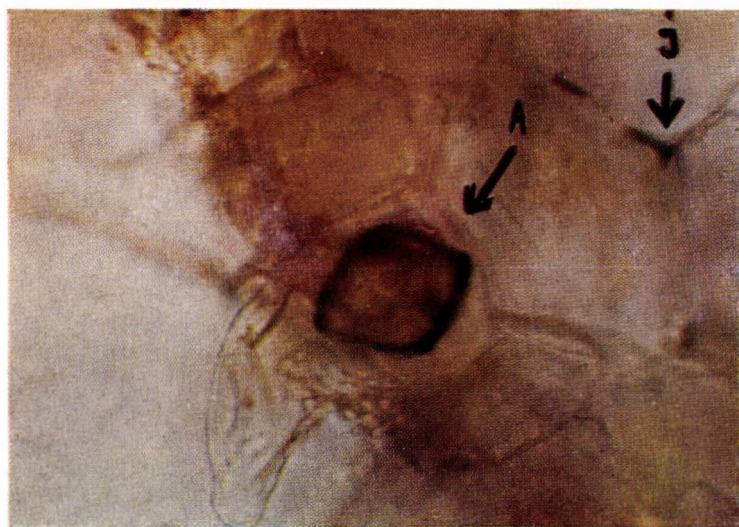
Fig. 8. Alkaloid crystal of enormous size in a hair cell root; treated with MAYER reagent (A), and alkaloid positive intercellulars (I). Magn. = obj. 40 × oc. 5
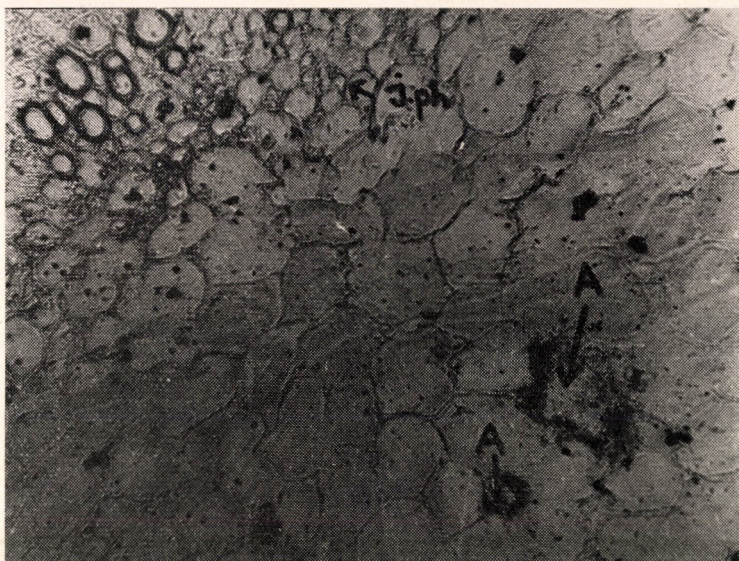
Fig. 4a. Alkaloid crystals in pith of idioblast the stem. I. ph = intraxylar phloem. Magn. = obj. 8 × oc. 5. autoradiogram
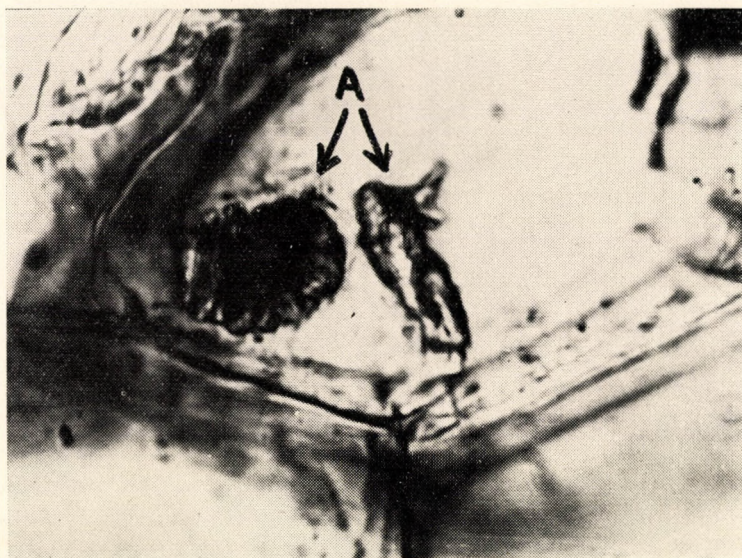
Fig. 5. Two alkaloid crystals in the parenchymatous cells of the pith. Immersion photograph Magn. = obj. 90 × oc. 15

rarely empty either in young or in old organs. They are well absorvable — mostly in longitudinal sections — as elongated interstices, like passes between neighbouring cells. Subulate crystals are observable in them (Figs 6 and 7),

which — owing to the refraction of light conditions caused by narrow space — are mostly of black or dark gray colour and produce alkaloid positive reaction in every case. They turn a lively red colour with DRAGENDORFF reagent, yellow with MAYER reagent and picric acid, and black with hexachloroplatium.

The presence of alkaloid prismatic single crystals of large size is observable already in the parenchymatous cells in the surroundings of the vascular
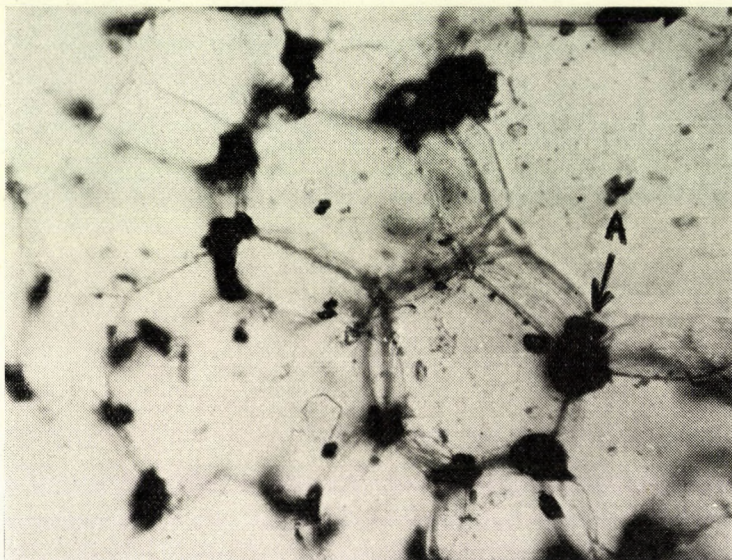
Fig. 6. Intercellulars containing alkaloid crystals in the dilatational parencyhma tissue of the root, cross-section (treated with MAYER-reagent). Magn. = obj. 20 × oc. 5

tissue in young seedlings. Irregular, large alkaloid grains may also occur, mainly in the secundary vascular tissue of the older root, in the vicinity of the parenchymatous cells surrounding the wide lumen tracheae and often performing local meristematic activity (JACKSON—WALLIS 1955). It can be observed that these be of whatever size, stain conspicuously with alkaloid reagents, while the typical Ca-oxalate rosettes of the foliage leaf remain unstained.

The anatomical characteristic that alkaloid crystals are demonstrable also in certain cells of the rhizodermis in young seedlings (Fig. 8) is noteworthy and in our opinion it may lead to interesting results also from the point of view of association biology.

The glandular hairs of the plant produce definite alkaloid reactions. These hairs are of two kinds: innoxia hairs with one-celled head, and multicellulare petiole (VERZÁR-PETRI, SÁRKÁNY 1961) as well as the typical Solanaceous glandular hairs with multicellular head and short, often one-celled petiole. The alkaloid reaction is observable in the head cells of the hairs. No crystalline

alkaloid reaction is observable here. Assumably, this is in connection with the fact that the glandular hairs contain volatile oil and even grease-like substances, corroborated by the alcohol test, Sudane III reagent and several volatile oil reagents (TUNMANN—ROSENTHALER 1931). It can be inferred therefore that in them the alkaloids take another form, possibly dissolved in substances of a lipoid character.

Fig. 7. Phloem parenchyma containing alkaloid crystals, and alcaloid positive intercellulars. Cross-section from the stem. Magn. = obj. 20 × oc. 5

In the further experiments radioactive generally marked H^3-atropine was used. The aim was to trace the path and location of the radioactive alkaloid in the tissues of *Datura innoxia* and to compare the results with the experiences attained by the histochemical investigations, i.e. to evaluate the results together.

As is known, the second main alkaloid of *Datura innoxia* is l-hyoscyamine of which the raceme, optically inactive variety is atropine. According to certain authors, atropine develops in plants not only postmortally, but is present to a smaller extent — along with l-hyoscyamine — also in the living plant (EVANS 1966). On the basis of these it was hoped that conditions is in agreement with those in nature will be established during the experiments.

Contact macroautoradiography was mainly used. It could be shown that the plant took up and transported the radioactive alkaloid (Fig. 9). The specificativity of up-take was small, merely 0.04 per cent.

Similar observations were made, however, also by ROMEIKE and KOBLITZ (1970) in the tissue culture of *Datura innoxia* in connection with the radioactive
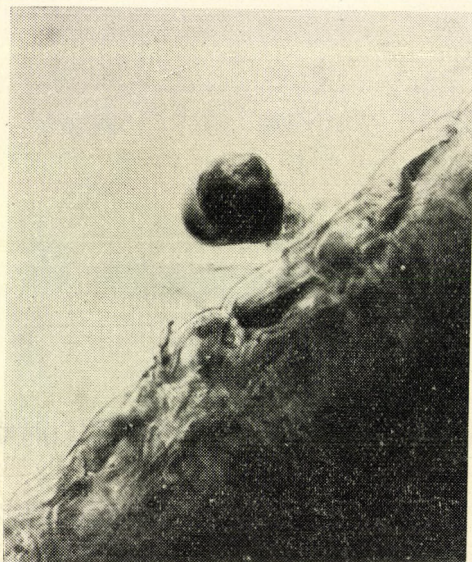
Fig. 9. Solanaceous glandular hair with alkaloid positive head, from the upper surface epidermis of the leaf. Magn. = obj. 40 × oc. 5

Fig. 10a. X-ray photograph of foliage leaf having absorbed triciated atropinborate
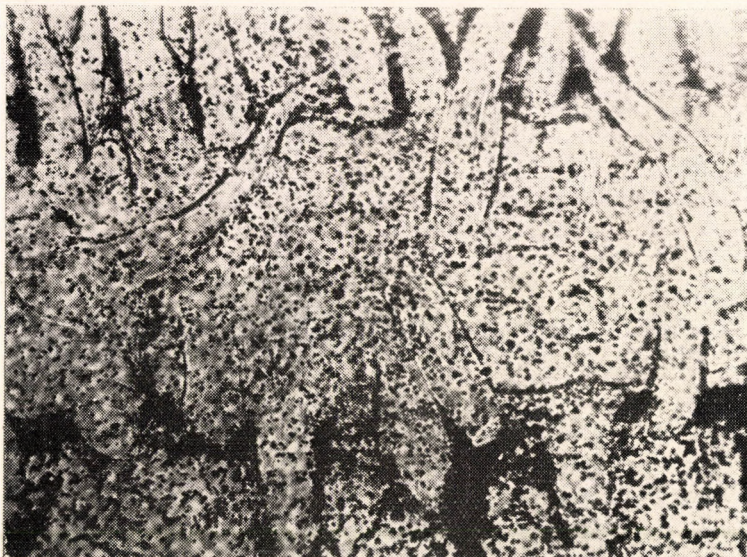
Fig. 10b. Contact histoautoradiogram of the midrib with simple cover-hairs (a) and glandular hairs (b. c.). Magn. = obj. 40 × oc. 5
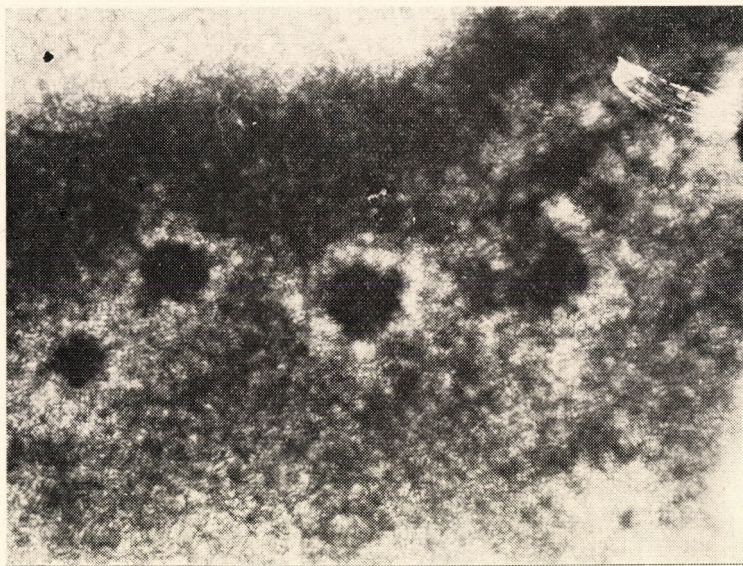
Fig. 10c Radioactiv glandular hairs (1, 2)

hyoscyamine up-take; they stated that above a certain basic level the plant rejects the alkaloid dosed in.

It was found from the autoradiogram of the foliage leaf that the radioactive alkaloid is not equally distributed in the tissues of the leaf. Most of it
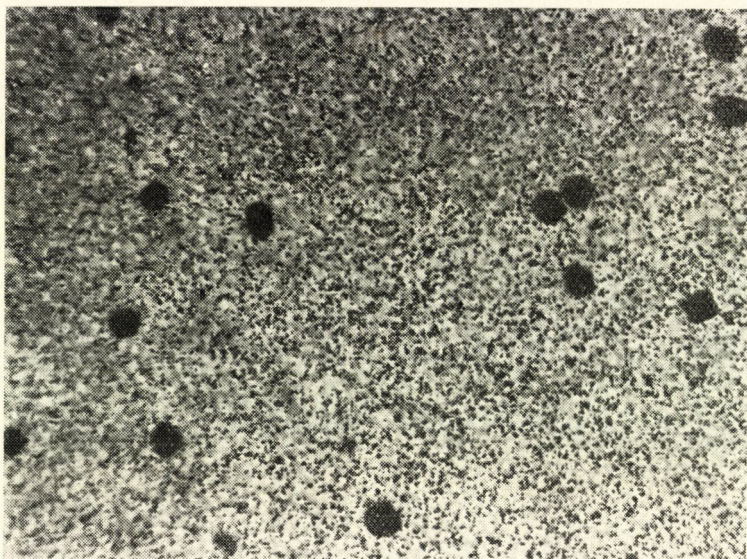
Fig. 11a. Surface of stem epidermis with radioactive glandular hairs. Contact technique. Magn. obj. 8 × oc. 5

Fig. 11b. Same as in Fig. 11a; from inactive material, treated with DRAGENDORFF reagent

was contained in the venous system. As a consequence, the venation conspicuously blackened on the X-ray film. As seen under the microscope, the little glandular hairs among and at the roots of the lengthy, flagelliform cover hairs, standing thickly along the midrib edge as well as the glandular hairs of *Datura innoxia*, became strongly radioactive (Figs 10, 11). Accordingly there is no

doubt that the radioactive alkaloid absorbed by the plant reaches the epidermis of the plant, and even the cells generating the hairs, through the transporting path.

As regards the distribution and location of the radioactive alkaloid, interesting observations could be made also in the stalk tissues of *Datura innoxia*. It was observed that the radioactive compound is conveyed through the transport path; this is confirmed by the fact that the xylem elements are radioactive (Fig. 12). The path of the radioactive substance starting from the
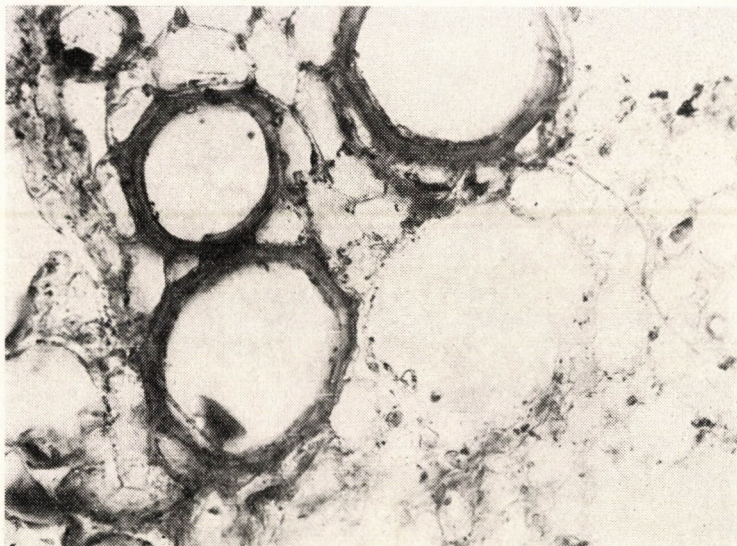
Fig. 12. Radioactivity spreading in the vascular tissue of the stem (histoautoradiogram). Magn. = obj. 40 × oc. 8

inner phloem towards the cells holding the crystals of the pith can be well traced. These crystals-holding cells, which produced a positive alkaloid reaction in the histochemical investigations, are definitely distinguishable in the histoautoradiograms. It is observable that some of them become charged with radioactive crystals, and these can also be distinguished in the neighbouring cells. This indicates that the radioactive alkaloid absorbed in dissolved state by the plant reaches the pith of the plant, where it crystallizes. All this happens mainly in the cells that have meanwhile accumulated the alkaloids, but crystallization also takes place in the surrounding cells, and even the content of intercellulars belonging to the surrounding cells is becoming radioactive (Figs 13 and 14).

It may also occur that the alkaloid crystals are found along the cell wall, in the narrow cytoplasma-lining, or in the individual poles of the cell (Fig. 15).
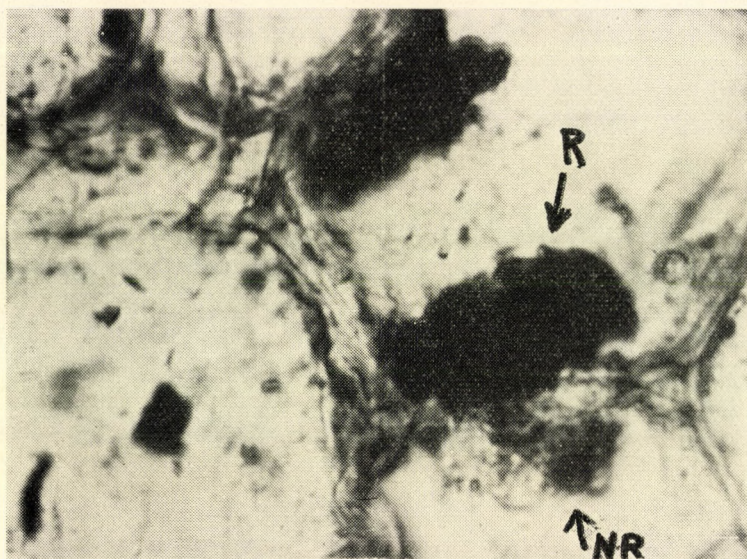
Fig. 13. Radioactive (R) and non-radioactive (NR) alkaloid crystals from the primary xylem of the stem, after absorption of triciated atropine borate. Immersion photograph. Magn. = obj. 90 × oc. 5
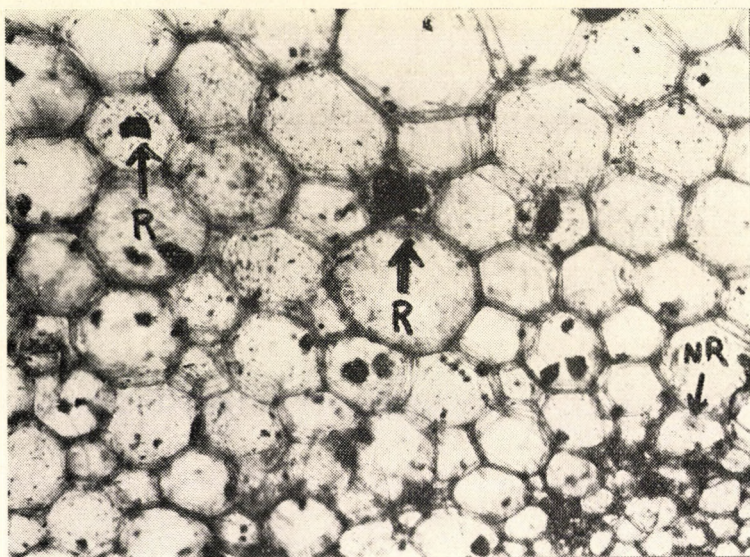
Fig. 14. Radioactive and non-radioactive alkaloid crystals from the pith of the stem. Magn. = obj. 8 × oc. 5

A fairly frequent phenomenon is the accumulation of radioactivity in the *intercellulars* of the parenchymatous cells of the primary cortex as well as in such wall cell parts through which plasmodesm penetrate into the neighbouring

Fig. 15. Bipolar position of radioactive and non-radioactive alkaloid crystals in the pith parenchyma of the stem. Histo-autoradiogram. Immersion photograph. Magn. = obj. 90 × oc. 5
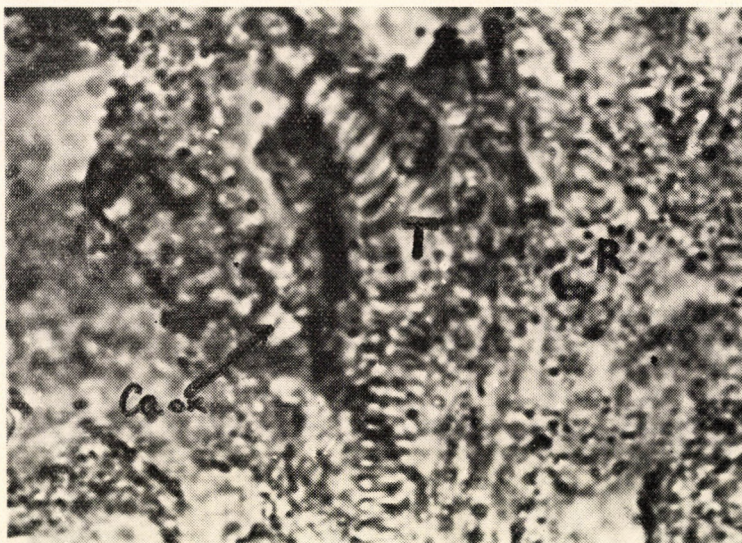
Fig. 16. Distribution of radioactivity originating from triciated atropine in the parenchyma around the midrib of *Datura innoxia.* T = trachea, Ca-ox = calcium-oxalate inactive crystal, R = radioactive granula. Magn. obj. 90 × oc. 5

cells. This kind of radioactivity distribution allows for the inference that there is also transversal movement in the substance (Fig. 16).

From the results of the investigations it has been inferred that in the tissues of *Datura innoxia* the localization of alkaloids takes place in definite

cells, in crystal form; or, it is eliminated from the cells into the intercellulars. Alkaloid precipitation in the glandular hair may also occur. From all these it could be inferred that the alkaloids in *Datura innoxia* are compounds that are excreted from metabolism. This is definitely verified by anatomical characteristics.

Retreating the question of excretion in plants, on the basis of MOTHES' biochemical observations, FREY-WISSLING (1970) considers the alkaloids typical excreta, but he remarks that concrete histological results are still lacking in this field. It is hoped that the observations discussed above (and the results in the press of my previous investigations into the same subject but concerning indol and tobacco as well as actinidine-type alkaloids) will bring us nearer to the knowledge of localization of the alkaloids in the tissues of plants.

Summary

The localization of alkaloids in various tissues of the vegetative organs of *Datura innoxia* Mill. was examined in histoautoradiographic investigations with by the application of general marked radioactive triciated atropine, and histochemical methods.

It was stated that alkaloids are observable in the glandular hairs of the epidermis — in the intercellular spaces in primary cortex and the pith parenchym, and in the root hairs of the rhizoderm. They are in liquid state in the glandular hairs and in crystalline form in the other tissues. The alkaloids crystallize in definite cells, idioblasts, or they are excreted in the intercellulars of the phloem and pith parenchyma.

The localization of the radioactive alkaloids occurs into the same places as known for inactive alkaloids. Besides the transportation of radioactive alkaloids was also observable in the elements of the xylem and also their transversal movement towards the outer tissue areas and the pith tissue.

Anatomical characteristics indicate the secerning of the alkaloids from the metabolism of the plants.

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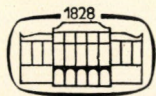
INDEX

The Microflora in the Settling and Subsoil-Water Enriching Basins of the Budapest Waterworks

A comparative study in ecology, limnology and systematics

by T. Hortobágyi

Biospherical pollution and the eutrophization of natural waters are the problems of today. The author introduces in his present work the biocoenoses of the Budapest Waterworks. Detailed discussion is given on water production, on the physical and chemical condition of the basins, on the author's limnological and biological statements. In the taxonomical part, he deals with 415 taxa belonging to 116 genera beautifully illustrated in 610 original drawings. The author ascertained 238 taxa, new to the flora of River Danube; 58 taxa proved to be new to science. The work is concluded with the evaluation of the collectings; the individual phytocoenoses are compared in time and space.

In English · Approx. 240 pages · Cloth

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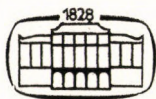
A. O. Horvát

DIE VEGETATION DES MECSEKGEBIRGES UND SEINER UMGEBUNG

In deutscher Sprache · Etwa 350 Seiten · 135, z. T. mehrfarbige Abbildungen 56 Tabellen · 17 × 25 cm · Ganzleinen

Das Werk umfaßt, zumeist auf grund eigener Forschungen des Verfassers, die die Pflanzendecke des Mecsekgebirges und seiner Umgebung betreffenden Kenntnisse. Das Wertvollste an ihm ist die Vegetationskarte, deren Bearbeitung im Maßstab 1 : 10 000 fast ein Jahrzehnt in Anspruch nahm und jetzt im Maßstab 1 : 50 000 zur Herausgabe gelangt. Es kommt selten vor, daß die Vergesellschaftung der Wälder eines Gebirges von einer so ausgedehnten Fläche von mehr als 100 km^2 bis auf Waldtypen detailliert zur Bearbeitung und zur kartographischen Aufnahme gelangt. Daraus läßt sich die prozentuale Verteilung der verschiedenen Waldtypen in diesem Gebiet gut entnehmen. Das Gebiet ist bekanntlich reich an submediterranen und südöstlich beheimateten Floraelementen und an deren charakteristischen Vegetationstypen. Hieraus ergeben sich abwechslungsreich-farbige Pflanzengesellschaften von teils mitteleuropäischen, submediterranem, kontinentalem und auf dem Balkan beheimatetem, Charakter.

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VERLAG DER UNGARISCHEN AKADEMIE DER WISSENSCHAFTEN
BUDAPEST

INDEX HORTI BOTANICI UNIVERSITATIS HUNGARICAE QUAE PESTINI EST. (PEST, 1788)

Facsimile edition

edited and the Postscript written by Sz. Priszter

The original work was compiled and edited by J. J. Winterl, Austrian by birth, the first professor of botany and chemistry in the University of Pest. The Index was issued in 1788 with the aim to bring information on plants found in the Botanical Gardens of that time. More than 1700 plants comprising the stock of the Botanical Garden in Pest at that time, are listed in the Index together with nearly one hundred plants that were considered new by Winterl; twenty-six species are illustrated on copperplate engravings. The facsimile edition is complemented by a study of some 30 pages in English, ensuring the use of the Index for the readers in our days.

In Latin with an English postscript

Approx. 180 pages · Cloth

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Budapest

ACTA BOTANICA
ТОМ 18 — ВЫП 1—2

РЕЗЮМЕ

ПЕТЕР МЕЛИУС

Р. ШОБ

По поводу 400-летней годовщины смерти Петера Мелиуса автор статьи вспоминает о его деятельности. Его труд **«Herbarium»**, 1578 был первой книгой о ботанике на венгерском языке, вслед за Лоницером, и заодно первой венгерской сельскохозяйственной и медицинской книгой. Петер Мелиус был в XVI столетии одним из самых знаменитых реформатских миссионеров, епископом города Дебрецен.

АФРИКАНСКИЕ МХИ, СОБРАННЫЕ ДР-ОМ ДЕНЕШ БАЛАЖ

М. БИЗОТ

В ходе постранного африканского путешествия в Алижире, Камеруне, Кении и Эфиопии, венгерский географ д-р Д. Балаж собрал богатую коллекцию мохообразных. Д-р Поч (Специальное заведение по обучению преподавателей, Эгер, Венгрия) обратился ко мне с просьбой провести анализ материала. В результате исследования обильного материала предоставилось возможным описать ряд новых видов и видоизменений: ***Acanthocladium Cuynetii***, ***Acroporium Pocsii***, ***Didymodon rigidulus*** **var.** ***acutus***, ***Fabronia Pocsii*** **var.** ***cameruniae***, ***Fissindens Cuynetii***, ***Hookeriopsis Balazsii***, ***Leptodontium*** **(?)** ***Allorgei Pogonatum afrournigerum***, ***Rhynchostegium Jovet-Astii***, ***Tortula Pierrotii***, ***Tortula Toutonii***.

Было установлено, что коллекция содержит виды, происходящие из далекого прошлого, как напр. **Thuidum borbonicum**, и что некоторые виды являются синонимами; так напр. **Stereophyllum radiculosum** представляет собой синоним вида ***Stereophyllum indicum*** и ***Stereophyllum nitens*** является синонимом различных африканских видов. Кроме того, др-у Д. Балаж представилась возможность собрать приносящий плоды вид ***Fissidens subarboreus***, на основе чего можно подтвердить представление Потие де ла Варда о роде **Monkemeyera**. Для этого рода характерен перистом с целыми зубчиками, и он связан незаметными переходами с родом **Fissidens**, имеющим раздвоенные посередине зубчики.

НОВЫЕ РАСТЕНИЯ КУБЫ, II

А. БОРХИДИ и О. Г. МУНИЗ

В настоящей второй публикации серии статей авторы дают описание дальнейших 16 новых таксонов, обнаруженных в Кубе в ходе научных экспедиций по картированию растительности. Наряду с этим в статье подвергаются таксономической ревизии некоторые сомнительные полиморфические виды флоры Кубы, в том числе виды ***Amyris stromatophylla*** **P. Willx.**, и ***Tabebuia petrophila*** **Green.**, и приводятся также фототипы или фотоизотипы некоторых прежних таксонов (**Borhidi, A.—Muñiz, O.: New Plants in Cuba I; Acta Bot. Acad. Sci. Hung. 17, 1971, 1—36**).

Новые таксоны следующие: **Rutaceae:** *Amyris* (2 ssp.); **Euphorbiaceae:** *Leucocroton* (1 sp.), *Platygyne* (2 sp.); **Bucaceae:** *Buxus* (1 sp., 1 var.): **Celastraceae:** *Gyminda* (1 sp.); **Sapindaceae:** *Thouinia* (1 var.); **Rhamnaceae:** *Rhamnidium:* (1 sp.); **Bignoniaceae:** *Tabebuia* (1 ssp.); **Gesneriaceae** *Rhytidophyllum* (1 sp.); **Rubiaceae:** *Exostema* (1 var.); **Asteraceae:** *Heptanthus* (1 sp.), *Eupatorium* (1 sp.), *Vernonia* (1 var.).

ЦИТОФОТОМЕТРИЧЕСКОЕ ИЗУЧЕНИЕ СОСТАВА ДНК В ДИПЛОИДНЫХ ВИДАХ ЛЯДВЕНЦА (LOTUS)

О. Л. БОРШОШ

Проведено сравнительное цитофотометрическое исследование тринадцати диплоидных видов лядвенца (**Lotus**), у пяти из которых число хромосом составляет $2^n = 14$, а у восьми — $2^n = 12$. Для определения относительного содержания ДНК клеток автор использовала интегрирующий микроденситометр «GN 2». Измерения были проведены на делящихся клетках, находящихся в телофазе, взятых из конуса нарастания корня каждого исследовавшегося вида лядвенца.

У пяти видов с числом хромосом 2n = 14 величина абсорбции ДНК ядра клеток была более высокой (6,47—8,13), чем у восьми видов с числом хромосом 2n = 12 (2,97—4,39).

В целях определения относительной плотности содержания ДНК клеток автором было проведено сравнение относительных абсорбционных величин содержания ДНК каждого отдельного вида с 14 хромосомами с величинами каждого отдельного вида с 12 хромосомами, а также величин каждого отдельного вида с числом хромосом 2n = 14 со средним значением абсорбционных величин ДНК всех видов с числом хромосом 2n = 12. Порядок пяти видов с числом хромосом 2n = 14 от более низкой величины потностли ДНК к более высокой: ***L. edulis***, ***L. arenarius***, ***L. oraithopoides***, ***L. requienii***, ***L. cytisoides***.

ИЗМЕНЕНИЯ АНАТОМИИ ЛИСТЬЕВ И ФОТОСИНТЕЗА У ВИДА Quercus pubescens Willd ПОД ВЛИЯНИЕМ ФАКТОРОВ СРЕДЫ В РАЗЛИЧНЫХ ЭКОСИСТЕМАХ

I. Изменения анатомии листьев

Г. ФЕКЕТЕ и Й. СУЙКО-ЛАЦА

Целью авторов было выяснение вопроса, какие изменения наблюдаются по четырем анатомическим признакам листьев у вида ***Quercus pubescens*** под влиянием факторов среды. На основе комбинации двух уровней освещения и водоснабжения авторы выбрали четыре типа места произрастания, с которых собрали образцы.

Соотношение палисадной/губчатой паренхим и размер клеток мезофилла аналогичным путем реагируют на комбинацию двух факторов. Только свет оказывает достоверное влияние на соотношение палисадной/губчатой паренхим. На мезофилл оба фактора оказывают достоверное действие, тогда как на межклеточное соотношение и частоту устьиц только фактор воды оказывает достоверное влияние. При более низком уровне интенсивности света анатомические признаки листьев более стойкие против изменений водоснабжения в почве, чем при более высоком уровне освещения. Межклеточное соотношение находится в корреляции с размером мезофилла и частотой устьиц.

Авторы придерживаются того мнения, что мезофилл можно рассматривать не только как единицу снабжения газом, но также как единицу производства и транспорта органического вещества.

ИЗУЧЕНИЕ ТОКСИЧЕСКОГО ДЕЙСТВИЯ СОЛЕЙ МЕДИ НА КУКУРУЗЕ

В. ФРЕНЬО и Т. Д. НИНХ

Сильно разбавленный раствор медного купороса и других солей меди стимулируют фотосинтез, однако, по истечении более длительного времени на листьях наблюдаются симптомы интоксикации. Согласно исследованиям авторов в таких случаях отравление вызывается не медью, а в случае применения медного купороса хорошо видное повреждение можно отнести к действию серной кислоты. В этом установлении совершенно новым является только то, что серная кислота, происходящая из гидролиза медного купороса в такой очень незначительной концентрации не может вызвать повреждения такого большого размера.

Авторы объясняют отравление тем, что вследствие избирательного поглощения ионов и связанного с этим ионного обмена непрерывно образуются новые количества H_2SO_4, причем их агрессивное действие достигает такой степени, которая вызывает повреждение.

НИЖНЕПАННОНСКИЕ ДИАТОМЕИ ИЗ НЕОГЕННОГО БАССЕЙНА У СЕЛА ЧАКВАР

Часть II

М. ХАЙОШ

Вторая часть работы содержит краткое изложение остатков порядка **Pennales** штамма ***Bacillariophyta***, а также остатков ***Phytolitharia***, ***Tintinnidum*** и ***Porifera***, встречавшихся в комплексе остатков.

На основе процентной оценки можно отметить, что для остатков изучаемой свиты отложений характерно господствующее количество мезогалинных, литоральных и планктонных форм.

Виды **Actinoptychus trilobatus n. sp.** и ***Consinodiscus jambori* n. sp.** указывают на нижнепаннонскую эпоху и на мезогалинную фацию, что доказывается также макрофауной. Вид ***Actinoptychus trilobatus* n. sp.** показывает родство с морским видом ***Actinopstychus senarius* (Ehr.) Ehr.**

Исследуемый бассейн повидимому был опресняющейся, отшнуровавшейся морской бухтой, возможно лагуной, в которой на опреснение влияла близость берега.

ТАКСОНЫ CHLOROCOCCALES ИЗ БАССЕЙНОВ ДЛЯ ОБОГАЩЕНИЯ И ОСАЖДЕНИЯ ГРУНТОВОЙ ВОДЫ БУДАПЕШТСКОЙ ВОДОПРОВОДНОЙ СТАНЦИИ

Т. ХОРТОБАДЬИ

Приводится описание 20 новых таксонов, выделенных из бассейнов Будапештской водопроводной станции, питаемых водой Дуная, в том числе: 7 видов, 3 видоизменений и 10 форм. Сборы проводились в 1968 и 1969 гг. Во время исследований величина pH воды колебалась от 7,48 до 8,98. Глубина воды в бассейнах была 70—120 см. Физические, химические и лимнологические условия бассейнов обсуждаются более подробно в статье «**Mikroflora der Absetz- und Grundwasseranreicherungsbecken der Hauptstädtischen (Budapester) Wasserwerke**”, **Hidrológiai Közlöny 50/11 p. 481—484, Budapest 1970.**

Новые таксоны следующие: ***Chodatella budapestiensis* Hortob.**, ***Elakatothrix gracilis* Hortob.**, ***Micractinium crassisetum* Hortob.**, ***Occystidium polymammilatum* Hortob.**, ***Quadricoccus ellipticus* Hortob.**, ***Tetrastrum parallelum* Hortob.**, ***Tetrastrum tenuispinum* Hortob.**;

***Chodatella budapestiensis* Hortob. var. *trisetigera* Hortob.**, ***Crucigenia truncata*, G. M. Smith var. *scutata* Hortob.**, ***Scenedesmus denticulatus* Lagerh. var. *disciformis* Hortob.**;

***Chodatellopsis elliptica* Korsch. f. *undulata* Hortob.**, ***Lagerheimia trigona* Hortob. f. *longispina* Hortob.**, ***Lagerheimia wratislawiensis* Schreed. f. *gracilis* Hortob.**, ***Pediastrum Boryanum* (Turp.) Menegh. f. *flexuosum* Hortob.**, ***Pediastrum duplex* Meyer var. *gracillimum* W. et W. f. *danubiale* Hortob.**, ***Pediastrum tetras* (Ehr.) Ralfs var. *tetraodon* (Corda) Hansg. f. *globosum* Hortob.**, ***Tetraëdron caudatum* (Corda) Hansg. var. *incisum* Lagerh. f. *punctato-flexocaudatum* Hortob.**, ***Scenedesmus decorus* Hortob. var. *bicaudatus* Hortob. f. *heterogranulatus* Hortob.**, ***Scenedesmus ellipsoideus* Chod. var. *bicaudatus* Hortob. et Németh f. *granulatus* Hortob.**, ***Scenedesmus intermedius* Chod. var. *bicaudatus* Hortob. f. *danubialis* Hortob.**

ИЗУЧЕНИЕ ДЕЙСТВИЯ 2,4-Д НА НЕКОТОРЫЕ ПАРАМЕТРЫ ОБМЕНА ВЕЩЕСТВ ПРОРОСТКОВ Vicia faba

М. ХОРВАТ, Д. НАДЬ и И. РОЙИК

Корни проростков *Vicia faba* были подвергнуты действию вредной для растения концентрации (28 ppm) раствора Диконирт. Под влиянием Диконирта повысилась активность двух важных ферментов, пероксидазы и оксидазы аскорбиновой кислоты, участвующих в терминальном окислении. Этот процесс предположительно обуславливается окислением редуцированных продуктов посредством механизма, отличающегося от нормального обмена веществ. Торможение синтеза пигментов сказывается в снижении общего содержания пигментов, вызванном действием Диконирта.

ИЗУЧЕНИЕ УЛЬТРАСТРУКТУРЫ ПЫЛЬЦЕВЫХ ЗЕРЕН АНГИОСПЕРМАТОФИТОВ НИЖНЕГО ЭОЦЕНА

М. КЕДВЕШ и А. ПАРДУЦ

В ходе изучения ультраструктуры пыльцевых зерен покрытосеменных растений нижнего эоцена проводилось исследование девяти видов. Дается описание одного нового рода-формы (***Transdanubiaspollenites***) и одного нового вида-формы (***Tricolporopollenites sooi***), а также и их ультраструктуры. Из видов-форм, описанных раньше исключительно только на основе микроскопических исследований, микроскопический диагноз видов ***Basopollis basalis*** **Pf. 1953** и ***Diporites iszkaszentgyörgyi*** **Kds. 1965** дополняется данными электронномикроскопического анализа.

СВЯЗЬ МЕЖДУ СТРУКТУРНЫМИ И ФУНКЦИОНАЛЬНЫМИ ХАРАКТЕРИСТИКАМИ СТЕПНЫХ ЛЕСОВ В ВЕНГРИИ

И. ПРЕЧЕНЬИ

Корреляции между доминантным весом, разнообразием (структурные характеристики) и продуктивностью, балансом энергии, эффективностью и временем оборота (функциональные характеристики) были изучены на основе измерения трехлетней фитобиомассы в двух степных растительных сообществах. Между доминантным весом и разнообразием была установлена обратная взаимосвязь. За исключением времени оборота все функциональные характеристики показывают обратную взаимосвязь с доминантным весом. Функциональные характеристики показывают прямую связь между собой, за исключением времени оборота, находящегося в обратной корреляции с остальными функциональными свойствами. Результаты исследований отчасти находятся в противоречии с некоторыми прежними наблюдениями.

ДЕЙСТВИЕ ГЕРБИЦИДА НА РЕДУКЦИОННОЕ ДЕЛЕНИЕ Vicia faba

И. РОЙИК, М. ХОРВАТ и И. ЛОНТАИ

Авторами было изучено действие Диконирта, натриевой соли 2,4-дихлорфеноксиуксусной кислоты, на редукционное деление *Vicia faba*. В подвергавшихся действию Диконирта клетках, прохождение помимо уменьшения числа делящихся клеток мейоза также оказалось ненормальным. Хромосомы слипались, становились узловатыми, наблюдалось образование хроматиновых телец, а также неравномерное распределение хроматинового вещества.

NOMINA NOVAE

Р. ШОÓ

В прежних сообщениях, особенно в серии **Species et combinationes novae I—X (Acta bot. Hung. 9 (1963) — 17 (1971)** у многочисленных таксонов не было приведено места сбора, названия собирателя и места хранения типа, а иногда (в отдельных статьях журнала **Bot. Közl.**) и базионимы. Не принимая во внимание данные новых комбинаций, имеющих значение формы (они не играют роли) автор дополнительно сообщает данные других, неполно сообщенных таксонов, которые теперь также являются **nomina rita publicata.**

ПОЛОВАЯ КОРРЕЛЯЦИЯ В САМООПЛОДОВОРЯЮЩИХСЯ И САМОБЕСПЛОДНЫХ СОРТАХ НЕКОТОРЫХ ВИДОВ ПЕРСИКА

Д. ШУРАНЬИ

Анализ цветков самооплодотворяющихся и самобесплодных сортов персика показал, что пестики самооплодотворяющихся сортов более длинные, чем пестики самобесплодных сортов того же вида. В противоположность этому у самобесплодных сортов

число тычинок больше, чем у самооплодотворяющихся сортов. Между самооплодотворяющимися и самобесплодными сортами отдельных видов наблюдалось достоверное различие по коэффициенту числа тычинок и длины пестика.

Между длиной пестика и числом тычинок культурных сортов персика доказано существование отрицательной взаимосвязи. Эта взаимосвязь различна у самооплодотворяющихся и у самобесплодных сортов, и на основе коэффициента становится более показательным различие между самооплодотворяющимися и самобесплодными сортами персика.

ДЕЙСТВИЕ АРКТИИНА НА ВСХОЖЕСТЬ СЕМЯН, НА ТКАНИ КОРНЕЙ И НА НУКЛЕИНОВЫЕ КИСЛОТЫ

М. САБО, Г. ЛАЗАР, Ш. ГУЛЬЯШ и А. ГАРАИ

Работа разделяется на три части, а именно: а) на предоставление новых данных о связи между годичным ритмом всхожести и содержанием арктиина. Авторы определяли содержание арктиина в отдельных органах и установили хемотаксономическую связь между концентрацией арктиина и типом цветков *Compositae*. б) Во второй части работы показывается с помощью гистологических исследований эффект арктиина на структуру ткани корня. В структуре ткани стебля под влиянием арктиина не наблюдается существенного изменения. в) Исследованиями циркулярного дихроизма доказывается, что арктиин вступает во взаимодействие с нуклеиновыми кислотами. Природа этого взаимодействия неизвестна, однако можно установить, что в присутствии арктиина ориентация нуклеиновых кислот (в довойной геликс?) повышается.

РЕГУЛИРОВАНИЕ РОСТА ТКАНЕЙ ТАБАКА ПРИ ПОМОЩИ ЦИТОХИНИНА И АУКСИНОВ

И. Л. СИРАКИ и М. МАРОТИ

Авторами было изучено регулирование роста изолированных тканей табака (*Nicotiana tabacum* L.) в зависимости от различных концентраций и комбинаций концентраций ауксинов (индолуксусная кислота, ИАА, дихлорфеноксиуксусная кислота, 2,4-Д) и бензимидазола (БИА). Цель экспериментов получить данные о действии, оказанном применяемыми соединениями на рост тканей, и о механизме их действия, чтобы подкрепить цитохининоподобное действие бензимидазола. Из результатов можно установить, что ИАА и БИА в зависимости от концентрации стимулируют рост тканей, в то время как 2,4—Д в зависимости от применяемых концентраций давала кривую максимума. При одновременном применении ИАА и 2,4—Д проявляется антагонизм, так как ИАА понижает стимулирование роста тканей, вызванное наиболее эффективным соединением (2,4—Д), а торможение, оказанное изолированным применением 2,4—Д не может быть уравновешенным даже применением наиболее эффективной концентрации ИАА. При применении ИАА повышение роста тканей и увеличение содержания белков происходят параллельно, а при применении 2,4—Д содержание белков увеличивается при концентрации, торможащей рост тканей, значит, торможение роста тканей происходит не путем торможения синтеза белков. Число клеток, приходящихся на единицу веса, как правило, повышается, по мере повышения концентрации, значит, вес отдельных клеток уменьшается. При совместном применении БИА и ИАА выявляется аддитивное действие. При совместном применении БИА и 2,9—Д это действие не представляет собой общее явление. Несмотря на то, что БИА не является соединением с пуриновым остовом, на рост тканей он все же оказывает такой же эффект, как «истинные» цитохинины.

КРИТИЧЕСКАЯ РЕВИЗИЯ ВИДОВ АРУМ (ARUM) КАРПАТСКОГО БАССЕЙНА

А. ТЕРПО

Автор анализирует в первую очередь инфраспецифические таксоны и распространение вида *Arum maculatum*.. На основе морфологических, цитологических, биометрических и фенологических исследований он приходит к заключению, что в Карпатском бессейне

популяции, рассматриваемые как *Arum maculatum*, на меньшем ареале распространения, как напр. в юго-западной части Венгрии, на самом деле относятся к виду *A. maculatum* с числом хромосом 2n = 56, в то время как большинство популяций (обнаруживаемых почти во всем Карпатском бассейне) относится к забытому виду *A. alpinum*. Число хромосом *A. alpinum* 2n = 28, листья не пятнистые, длина цветочной стрелки почти одинакова с длиной листового стебля, кроющий лист зеленоватый (длиной в 8,0—12,0 см), *clava* небольшая, клубень плоско-овальной формы направляется косо вверх. Автор относит к этому виду в качестве инфраспецифического таксона *A. intermedium* Schur и *A. gracile* unverricht, дает описание гибрида между *A. maculatum* и *A. alpinum*, называя его *A. Soói* Terpó.

Приводится также обсуждение прочих, встречаемых в Европе таксонов (*A. italicum*, *A. Besserianum*, *A. orientale*).

ГИСТОХИМИЧЕСКОЕ И ГИСТОАВТОРАДИОГРАФИЧЕСКОЕ ИЗУЧЕНИЕ ЛОКАЛИЗАЦИИ АЛКАЛОИДОВ В ВЕГЕТАТИВНЫХ ОРГАНАХ *Datura innoxia Mill.*

Г. ПЕТРИ-ВЕРЗАР

Локализация алкалоидов в вегетативных органах *Datura innoxia* Mill. была изучена гистохимическими методами, а также гисторадиографией после всасывания радиоактивного атропина.

Для гистохимического исследования автор применяла реагенты Майера, Драгендорфа, Шейблера, гексохлороплатин и другие. Изотопные исследования проводились после всасывания меченого атропинбората, методом эмульсионной гисторадиографии.

Было установлено, что в растении алкалоиды располагаются в кристаллической форме в сердцевине и в паренхиме коры в обособленных идиобластах или межклеточных пространствах, а также в корневых волосках. Кроме того алкалоиды встречаются в жидкой форме в головчатых клетках железистых волосков.

Растение поглощает радиоактивный алкалоид, который транспортируется в ксилеме и перемещается в направление неактивных мест выделения, где он выделяется в форме, наблюдаемой в гистохимических исследованиях.

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EFFECT OF LIGHT INTENSITY ON DRY MATTER PRODUCTION AND ENERGY UTILIZATION IN TOMATO PLANTS

By

S. R. BAROOVA and I. HORVÁTH

DEPARTMENT OF BOTANY, ATTILA JÓZSEF UNIVERSITY, SZEGED

(Received: April 7, 1972)

The dry weight of both varieties reduced linearly along with the increase of shading intensity. Reduction rate in variety "Kecskeméti konzerv" was of a higher degree than in "Kecskeméti törpe". In field and in controlled conditions total carbohydrate concentration increases concurrently with the increase of illumination intensities, but inversely, it decreases in both varieties in nitrogen concentrations. Reduction of light energy by shading resulted in a generally lower degree of energy utilization. To changes in light relations both varieties reacted dissimilarly.

Introduction

A suitable intensity of light is an important factor for plants, since the photosynthesizing apparatus may suffer severe damages owing to too intense light effects. Injuries, indeed the destruction of cells may also occur after several hours of exposure.

Shading exerts complex effects in the field, altering not only the dispersion and angle of incidence of light, but also air movement and several other factors. Shading thus considerably influences the morphology, orientation etc. of the leaves. TAGEEVA et al. (1961), as well as VERKREK (1965), observed in tomato plants a decrease in dry weight, thinner leaf blades, and to some extent a reduction of the canopy in low light intensities. MÉSZÖLY (1966) found a correlation between light intensity, flowering, number, weight and value of fruits. BAROOVA et al. (1971) analysed the pattern of dry weight changes of tomato seedlings and light conditions, KRETCHMAN (1969) and SCHAFFER (1970) obtained more fruitsetting in tomato plants at high light intensities. The greatest utilization of light energy is commonly associated with a low illumination intensity, but a leaf optimum (L. opt) may evolve at any value of solar radiation. Below the leaf optimum light energy is not fully utilized, while above it the leaf tissues are not utilizing at the optimum rate (BLACK 1963).

Material and methods

Experiments were conducted both in the field and in controlled conditions with two varieties of tomato "Kecskeméti konzerv" and "Kecskeméti törpe". Different intensities of sunlight were attained by different degrees of shading. Illumination intensities were 30 to

40 per cent lower in the crop stand of "Kecskeméti konzerv" than in that of "Kecskeméti törpe". In the course of microclimate investigations soil and air temperatures, humidity content and light conditions of the crop stands were measured (WAGNER 1956).

In controlled conditions, experiments were carried out in light thermostate (HORVÁTH and KOLTAY, 1963). Plants were grown in sand cultures with seventy water holding capacity, from each variety two equally healthy plants grown in each pot. The plants were irrigated with distilled water daily and irrigated with Knop solutions once every week. The first observations concerning the open field experiment was made three months after the first transplantation (July 1970) and the second observations after two months following the first ones (September 1970). The plants grown in controlled conditions were examined when one month old.

With reference to energy utilization, chemical analyses of the dry matter were also done, from the different parts of the plant, for total carbohydrate and total nitrogen concentrations.

The plants from both varieties were examined in four repetitions.

Total carbohydrate concentrations of both investigated varieties were made according to DUBOIS et al. (1956), while the total nitrogen concentrations were determined, from the first observation material, according to KELLEY et al. (1946).

In determining the utilization of energy, light energy, total leaf area, growth area and light intensity received at different heights of the plant were taken into consideration. Energy utilization percentages were calculated as follows (MURATA et al. 1968)

$$\text{Eu} = \frac{\text{plant dry weight (gms)} \times 4000 \text{ (cal). } 100 \text{ (\%)}}{\text{available incident light (cal)}}$$

Results and discussion

In both varieties the dry weight of the aerial parts decreased owing to the shading treatment (Tables 1 and 2). A greater dry weight derives from a higher number of leaves and larger leaf area. Similar results were reported also by SESTAK and CATSKY (1962).

Table 1

Dry weight of aerial parts (gms)-field condition (1970)

Treatment (Shade)	"Kecskeméti konzerv"				"Kecskeméti törpe"			
	stem	leaf	fruits	total	stem	leaf	fruits	total
Without	29.1	25.4	44.7	99.2	11.4	19.3	18.5	39.2
Moderate	21.8	19.9	25.7	67.4	7.8	13.7	15.8	37.3
Heavy	14.0	14.7	7.9	36.6	5.8	12.3	9.1	27.2

SD 5% (total) "Kecskeméti konzerv": 3.17
"Kecskeméti törpe": 6.89

The optimum leaf area combined with good light absorption assures the balance of metabolic processes (MOSKHOV 1955, VERKREK 1965).

Concurrently with the rate of shading, dry weight decreases linearly in both varieties, by about 75% in "Kecskeméti konzerv" and about 50% in "Kecskeméti törpe". The results obtained from investigating the dry weight imply that the variety "Kecskeméti konzerv" requires more light than the variety "Kecskeméti törpe".

Table 2

Dyr weight of aerial parts (gms) controlled conditions

Light intensity (klux)	"Kecskeméti konzerv"			"Kecskeméti törpe"		
	stem	leaf	total	stem	leaf	total
3	0.03	0.03	0.06	0.02	0.02	0.04
9	0.23	0.33	0,56	0.12	0.20	0.32
12	0.37	0.53	0.90	0.20	0.36	0.56

SD 5% (total) "Kecskeméti konzerv": 0.13
"Kecskeméti törpe": 0.04

Table 3

Average number of fruits in the open field (Sept. 1970)

Treatment (Shade)	"Kecskeméti konzerv"	"Kecskeméti törpe"
Without	14	19
Moderate	9	14
Heavy	4	8

Table 4

Dry weight of fruits (gms) in the open field (1970)

Treatment (Shade)	"Kecskeméti konzerv"	"Kecskeméti törpe"
Without	44.7	18.5
Moderate	25.7	15.8
Heavy	7.9	9.1

The number of fruits per plant decreased in both varieties linearly and concurrently with the rate of shading (Table 3).

On the basis of fruit production (per plant) it can be stated that by variety "Kecskeméti konzerv" reacts to a greater degree to changes in light conditions (Table 4); accordingly this variety requires more light. In controlled conditions, dry weight increased concomitantly with the increase of illumination intensities in both varieties.

In control conditions, the carbohydrate concentrations of both stem and leaf were higher in both varieties than in plants grown in the field. For both open field and controlled conditions, however, the carbohydrate concentration of both stem and leaf reduce parallel with the reduction of illumination inten-
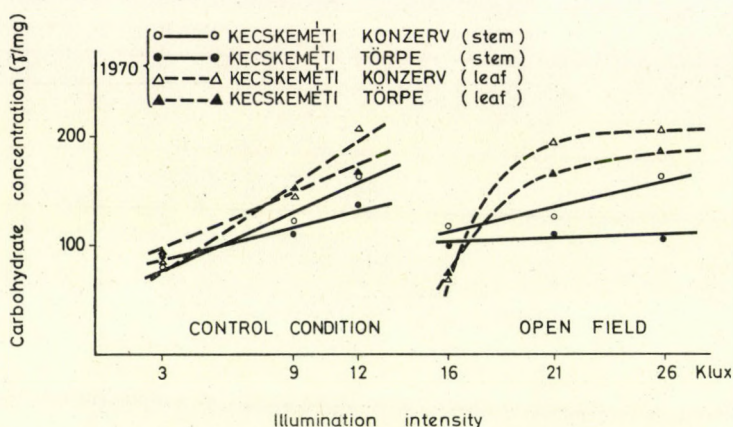
Fig. 1. Total carbohydrate concentration of stem and leaf in plants grown in controlled conditions and in the open field, under different illumination intensities
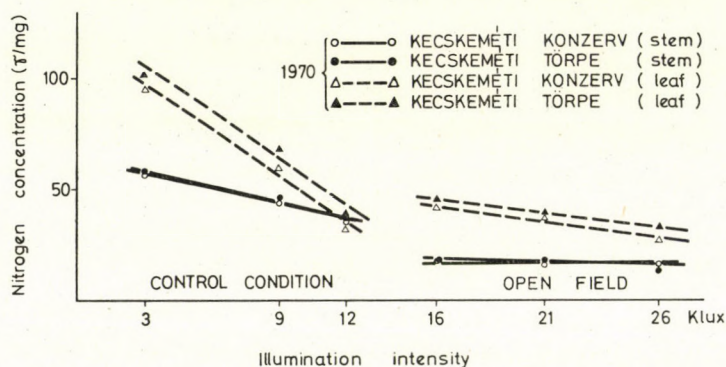
Fig. 2. Total nitrogen concentration of stem and leaf in plant grown in controlled condition and in the open field, under different illumination intensities

sities. In control conditions, reduction was linear both in the stem and the leaf of each variety. In the open field, a pronounced reduction was observed in the leaf of both varieties below illumination intensity 21 klux (Fig. 1).

The carbohydrate concentration of the variety "Kecskeméti törpe" was about 10—20 per cent lower than that of the variety "Kecskeméti konzerv". The nitrogen concentration was higher in both stem and leaf in controlled conditions. Nitrogen concentrations reduced linearly with the increase of illumination intensities in open field and also in controlled conditions. Reduction rate was higher in controlled conditions than in the open field (Fig. 2).

Carbohydrate concentrations in stem and leaf of both varieties increased with the increase of dry weight, both in the open field and in control conditions (Fig. 3).
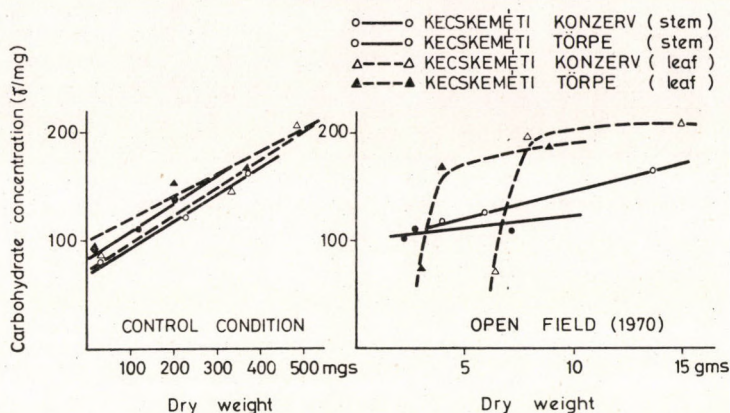
Fig. 3. Total carbohydrate concentration in relation to dry weight
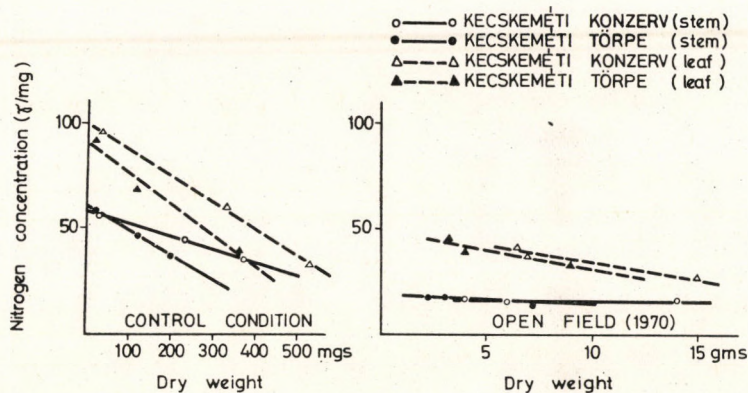
Fig. 4. Total nitrogen concentration of stem and leaf in relation to dry weight

In contrast to the total carbohydrate concentration, total nitrogen concentration decreases as a function of increasing dry weight.

In the open field, the concentration of total nitrogen as a function of dry weight is of a smaller rate; the reduction was linear and greater in the leaf than in the stem. In controlled conditions, the concentration of total nitrogen showed a stricter interrelationship with dry weight than in the open field.

In the open field, total nitrogen concentration was invariably lower (except the stem) in "Kecskeméti törpe" than in "Kecskeméti konzerv". In the stem, total carbohydrate concentration decreases concurrently with dry weight in both varieties; this correlation is less conspicuous (uniform) in the leaf. The soluble carbohydrate content of the leaves increases — following the dark period — rapidly by the effect of light; after reaching a certain value it hardly changes, owing to the complex relationship between the translocation of photo-

synthetic products from the leaf to the other parts of the plant and the photosynthetic productive capacity of the leaves.

This is related with the generalizable statement, given by HORVÁTH and SZÁSZ (1965) and ARNON (1961), that light intensity influences ATP and NADPH.

Table 5 summarizes the average energy utilization of both tomato varieties in the open field and in control conditions.

Table 5

Average energy utilization (in %) in the open field and in control conditions

Treatment	"Kecskeméti konzerv"	"Kecskeméti törpe"
Without shade	2.2	1.4
Moderate shade	2.2	1.7
Heavy shade	1.6	1.6
12 klux	15.5	12.9
9 klux	17.3	14.8
3 klux	21.6	15.9

The energy utilization of the plant depends on light intensity and leaf area. In both tomato varieties, the maximum energy utilization falls in the 0.3—0.6 leaf area index range. These results partly contradict those obtained by WATSON (1952), NICHIPOROVICH (1961), and HAYASHI (1966). The leaves of plants absorb light, especially in the growth zone. The assimilating tissues of these leaves utilize not only direct radiating energy but also that reflected from leaves lying below them.

Summary

1. The dry weight of both varieties decreased concurrently with the increase of shading. The relation is linear. The reduction rate in "Kecskeméti konzerv" is higher than in "Kecskeméti törpe". This indicates that the variety "Kecskeméti konzerv" requires more light.

2. On the basis of fruit production, a moderate shading is favourable for the variety "Kecskeméti törpe" in open field condition, but a more extensive shading decreases fruit production also in this variety. The reaction to light intensity is of a higher rate also on the basis of fruit production in the variety "Kecskeméti konzerv", hence this plant requires more light.

3. In the open field and in control conditions the total carbohydrate concentration increases parallel with the increase of illumination intensity in both varieties. The rate of increase is similar in both stem and leaf and linear with the increase of light intensity.

4. Total nitrogen concentration decreases concurrently and linearly with the increase of illumination intensity in both varieties. In control conditions, reduction is of higher degree than in the open field.

5. The reduction of light energy causes in general a lower degree of energy utilization. Both varieties react differently to changes in light conditions.

6. In the open field, energy utilization is rather determined by crop stand density and leaf area. The optimum leaf area index is about 0.3 and 0.6 for the variety "Kecskeméti törpe" and "Kecskeméti konzerv", respectively.

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LEAF ANATOMICAL AND PHOTOSYNTHETICAL REACTIONS OF QUERCUS PUBESCENS WILLD. TO ENVIRONMENTAL FACTORS IN VARIOUS ECOSYSTEMS

II. PHOTOSYNTHETIC ACTIVITY

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The authors examined the CO_2 incorporation ability (under the conditions of 10 000 lux light intensity and favourable water uptake) of the shade leaves in *Quercus pubescens* trees, growing in four different habitats determined according to a combination of two levels each of the water and light supply, in their relation to leaf anatomical characteristics. Three sample trees were chosen from each of the four habitats. The analysis of variance of the CO_2 incorporation data of the sample trees according to habitats is significant at 5%, level and when broken down to factors, the light effect shows a significance at 1%. The wood mass data of the sample trees run counter to the CO_2 incorporation capacity data of the leaves. The quantity of the water available in the soil effects the production of wood mass.

As regards the connection between anatomical characteristics and the quantity of incorporated CO_2, there is a significant correlation between the palisade/spongy parenchyma ratio and the $CO_2/dm^2/h$ incorporated at 1%, while the incorporated CO_2 mesophyll cell size, and the so-called intercellular ratio shows a significant connection with both at 0.1%. According to the results obtained by path analysis, it is the intercellular ratio of the leaf mesophyll which influences to the greatest extent the variability of the incorporated CO_2, on the other hand, the influence of the ratio of the palisade/spongy parenchyma is the smallest.

Material and method

The method of choosing the sample trees was described in a previous paper (Fekete and Szujkó-Lacza, 1972). The chosen 12 sample trees make possible the measuring of the effects of each of the 4 combinations (as habitats) of the two factors (A: "light"; B: "water") in 3 repetitions. The habitats are: 1. "Little light, much water", 2. "little light, little water"; 3. "much light, much water"; 4. "much light, little water". As regards the details of the measurements resulting in the qualification according to the levels of light and water, we refer again to the first part of our work. During the day of the investigation the light intensity values of the sample leaves of the trees in the first two habitats occurred between about 400 and 2500 lux, while in the third and fourth habitats between 1000 and 5500 lux. At spring time, in the state of undeveloped foliage fairly higher (daily maximal) light intensity values (4000—5000 and 8000—11 000 lux, respecti vely) are frequent.

The soil types of the first and third habitats are deep Ramann-type brown forest soils, with strongly developed, clayey, adobe B-level of good water capacity. The soils of the second

and fourth habitats are shallow black and brown rendzines with fragmentated limestone, their water capacity not reaching even half of that RAMANN-type soils.

Transitional stands between *Orno-Quercetum* and *Quercetum petraeae-cerris* associations grow in the first habitat, while in the second and third habitats *Orno-Quercetum* types with *Oryzopsis virescens* and *Vicia sparsiflora* respectively. In the fourth habitat karstic bush forest (*Çeraso-Quercetum*) develops. Anyhow the latter represents an ecosystem considerably differing from the others.

For measuring the CO_2 assimilation, on 26, August 1970, leaf samples were taken (4—5 leaves per sample tree) from the lowest thick branch of each tree; they were top leaves of top shoots. For one hour, at 10 000 lux light intensity, 12 leaf discs at a time were put to assimilate in a gas mixture of 0.4 mCi/mmole specific activity, which contained $^{14}CO_2$ of 0.25% concentration; parallel with this the extent of dark fixation was also measured. The quantity of the incorporated $^{14}CO_2$ was measured with the aid of an end-windowed GM tube of 11.2% efficiency. From the same leaves the chlorophyll components were also determined, after FRENCH (1960).

The analysis of variance of the measurement data in CO_2 assimilation and the calculation of the correlation coefficients between the examined four anatomical characteristics (palisade/spongy parenchyma ratio; determined on the basis of the leaf cross-section; the intercellulars/assimilating layers ratio, henceforth: intercellular ratio; the size of the mesophyll chamber;* stomatal frequency) were carried out after SVÁB (1967), while the path analysis after LE ROY (1960), and O'SVÁTH (1961).

The data of the wood mass measurements — to be considered as a supplementary investigation — were calculated on the basis of values of tree heigth measured on the spot, and of data on wood body diameter at chest height, from the felling table of Swappach (FEKETE 1951).

Results

In the evaluation, $^{14}CO_2$ values of incorporation by the leaves originating from the various habitats are related to leaf area. Having performed the analysis of variance, the result obtained was significant at 5% level; therefore, leaves of different structure are different also in their photosynthetic activities in experiments carried out under identical conditions. During a unit of time, the leaves originating from the third and fourth habitats with a high light level produce twice or thrice more than the ones obtained from a habitat with low light level. The results are given in Table 1.

Similar results and differences according to treatment pairs are obtained

Table 1

The quantity of CO_2 incorporated during one hour [10^{-4} *mmole/dm²/h*]

Habitat type	1	2	3	Mean
1	5.16	2.69	3.81	3.887
2	3.24	7.99	6.41	5.880
3	16.74	7.62	8.80	11.053
4	13.40	14.86	11.77	13.343

* Mesophyll chambers are mesophyll units closed by the bundle sheath extensions the ribs and the two epidermises.

Table 2

Analysis of variance of the data

Source of variability	SQ	df	MS
Total	243.099	11	
Habitat	174.354	3	58.12*
Factor A	160.525	1	160.525**
Factor B	13.760	1	13.760
A×B interaction	0.069	1	0.069
Error	68.745	8	8.590

Significance levels: *P = 5% **P = 1%

Table 3

The mean values (diagonally) from Table 1, their differences (semi-matrix on the right), and their significance levels (semi-matrix on the left side)

Habitat type	1	2	3	4
1	3.887	1.993	7.166	9.456
2		5.880	5.173	7.463
3	X		11.053	2.290
4	XX	X		13.343

^{x}P = 5% ^{xx}P = 1%

relating the incorporated CO_2 to the fresh leaf weight. On the other hand, when relating to the total quantity of the chlorophyll, the third habitat does not separate from the first two.

Besides measuring the CO_2 assimilation activity of the given leaves calculations were made to learn, how *Quercus pubescens* realizes its photosynthetic ability in the various habitats. The wood mass data of the sample trees of the approximately 60-year-old stock render information in this respect (Table 4).

When comparing the mean values by pairs, the values conspicuously separate according to the water factor (Table 6); the effect of factor B is significant also in itself (Table 5).

As a further step, starting from the consideration that the anatomical characteristics are in functional relationship with CO_2 incorporation and not with the subsistent production of many years, calculations of correlation coefficients were carried out between them. This is shown in the four correlation coefficients (with the significance levels) in Table 7; in the semi-matrix we

Table 4

Wood mass data of the examined sample trees in m^3

Habitat type	1	2	3	Average
1	0.20	0.46	0.60	0.420
2	0.06	0.11	0.15	0.107
3	0.29	0.39	0.25	0.310
4	0.09	0.06	0.08	0.076

Table 5

Analysis of variance of the wood mass data

Source of variability	SQ	df	MS
Total	0.340	11	
Habitat	0.243	3	0.081*
Factor A	0.014	1	0.014
Factor B	0.223	1	0.223**
A×B interaction	0.006	1	0.006
Error	0.097	8	0.012

Table 6

The mean values of wood mass data according to habitats from Table 4, their differences and the significance levels

Habitat type	1	2	3	4
1	0.420	0.313	0.110	0.344
2	XX	0.107	0.203	0.031
3			0.310	0.234
4	XX		X	0.076

Table 7

Correlation coefficients between the four anatomical characteristics and the incorporated CO_2 1: palisade/spongy parenchyma ratio; 2: mesophyll chamber size; 3: intercellular rate; 4: stomatal number; 5: incorporated CO_2 10^{-4} mmole/dm²/h

Habitat type	2	3	4	5
1	−0.742	0.375	0.252	0.753**
2		−0.627	−0.412	−0.949***
3			0.670	0.892***
4				0.367

**P = 1% ***P = 0.1%

also gave the correlation coefficient values of the anatomical characteristics between themselves.

It is to be seen from the Table (7) that the CO_2 incorporation shows the closest correlation with the mesophyll chamber size, and with the intercellular rate; the correlation is close and significant also, with the palisade/spongy parenchyma rate on the other hand, no reliable relationship could be pointed out with the stomatal number.

It is assumed that anatomical factors 1—4 function as causes influencing the rate of CO_2 assimilation (as a result). The path analysis [cf. LE ROY 1960; O'SVÁTH 1961; ZÓLYOMI—PRÉCSÉNYI 1970; PRÉCSÉNYI 1965 who was the first in using this method in Hungary for measuring the effect of environmental factors on plants] offers the possibility of estimating what percentages of the variability in the incorporated CO_2 values are influenced by the anatomical factors that have been included in the investigation. With the aid of the analysis we can estimate the percentage quotient of the direct and indirect effects of the various factors, as well as the effect of other factors not considered here (Table 8).

Table 8

Path coefficients of the factors examined and the percentage quotients of the various effects (for the key to the signs used cf. Table 7)

	Path coefficient	Effect, %
P_{15}	0.2206	4.87
P_{25}	−0.4526	20.48
P_{35}	0.8010	64.16
P_{45}	0.4122	16.99
Indirect		−10.41
Other		3.91
Total		100.00

An important result of the analysis is the showing that the main cause of the variability of CO_2 assimilation lies preponderantly in the rate of the intercellulars; its influence is of a positive trend. The influence of the mesophyll chamber size and the stomatal number is of nearly equal measure, lower and both of a negative trend; while the influence of the palisade/spongy parenchyma rate is positive but even lower.

With the aid of the path analysis established for the investigation of additive systems it is also possible to calculate the composition of the correlation coefficients (O'SVÁTH 1961) (Tables 9—12).

Therefore the increase in the palisade/spongy parenchyma rate raises the CO_2 incorporation only to a smaller-extent. It is clear that the indirect

Table 9

Breaking down of the correlation coefficient between palisade/spongy parenchyma rate and the incorporated CO_2 into its components

Palisade/spongy parenchyma rate CO_2 10^{-4}mmole/dm²/h	$r_{15} = 0.7530$
Effect of palisade/spongy parenchyma rate, directly	$P_{15} = 0.2206$
Effect of palisade/spongy parenchyma rate, indirectly	
through the mesophyll chamber size	$P_{25} \cdot r_{12} = 0.3358$
through the intercellular rate	$P_{35} \cdot r_{13} = 0.3004$
through the stomatal number	$P_{45} \cdot r_{14} = -0.1038$
	total: 0.7530

Table 10

Breaking down of the correlation coefficient between mesophyll chamber size and the incorporated CO_2 into its components

Mesophill chamber size CO_2 10^{-4} mmole/dm²/h	$r^{25} = -0{,}949$
Effect of mesophyll chamber size directly	$P_{25} = -0.4526$
Effect of mesophyll chamber size indirectly	
through the palisade/spongy parenchyma rate	$P_{15} \cdot r_{12} = -0.1637$
through the intercellular rate	$P_{35} \cdot r_{23} = -0.5022$
through the stomatal number	$P_{45} \cdot r_{24} = 0.1697$
	total: −0.9488

Table 11

Breaking down of the correlation coefficient between intercellular rate and the incorporated CO_2 into its components

Intercellural rate, CO_2 10^{-4} mmole/dm²/h	$r_{25} = 0.892$
Effect of intercellular rate directly	$P_{35} = 0.8010$
Effect of intercellular rate indirectly	
through the palisade/spongy parenchyma rate	$P_{15} \cdot r_{13} = 0.0827$
through the mesophyll chamber size	$P_{25} \cdot r_{23} = 0.2838$
through the stomatal number	$P_{45} \cdot r_{34} = -0.2762$
	total: 0.8913

ways are more important than its direct influence (through the mesophyll chamber size and the intercellular rate respectively).

The increase in the mesophyll chamber size reduces indeed considerably the CO_2 incorporation; however, the negative indirect influence through the intercellular rate is greater than even the direct influence.

Table 12

Breaking down of the correlation coefficient between the stomatal number and the incorporated CO_2 into its components

Stomatal number, CO_2 10^{-4} mmole/dm²/h	$r_{45} = 0.367$
Influence of the stomatal number, directly	$P_{45} = -0.4122$
Influence of stomatal number, indirectly	
through the palisade/spongy parenchyma ratio	$P_{15} \cdot r_{14} = 0.0556$
through the mesophyll chamber size	$P_{25} \cdot r_{24} = 0.1865$
through the intercellular ratio	$P_{35} \cdot r_{34} = 0.5367$
	total: 0.3666

It appears from Table 11 that the strong correlation between the intercellular rate and the CO_2 incorporation can be explained to a large extent by the direct influence of the intercellulars. Therefore intercellular space increases the capacity for CO_2 incorporation.

Surprisingly, an increase in the numbers of stoma decreases assimilation capacity. However, the positive correlations of the stomatal number, thus primarily its high positive correlation with the intercellular ratio, indirectly conceal the direct negative influence.

Discussion

The CO_2 assimilation of Quercus pubescens and the ecosystems

Considering the measurement results of the CO_2 incorporation experiment in the system and by the influence of the habitats, it can be seen from Table 1 that the leaves of individuals grown at high light intensity incorporate related to leaf area (and also weight) twice to three times the quantity of what is incorporated by individuals grown at low light intensity. The breaking down of the analysis of variance into factors (Table 2) shows that the effect of light on CO_2 incorporation is significant. Considering the intensity of CO_2 incorporation, similarly as in anatomical effects, primarily the influence of the fourth habitat appears also here. In a comparison between the ecosystems,

it can be inferred that the karstic bush forest ecosystem separates also in the photosynthetic activity of the leaf of the dominant *Quercus pubescens* from the *Orno-Quercetum*, in the given experimental conditions.

The light curve of the species has not been included (and we do not know about literature data relating to *Quercus pubescens* in this respect), but our results imply that the 10 000 lux light applied in the experiment may occur at that stage of the upward branch of the light curves where those of the light and shade leaves may have already intersected each other.

Although the nearly related *Quercus petraea*, becoming a strong competitor of *Quercus pubescens* in a habitat of low light intensity and a better water supply, is a "shade tolerant" species (at a higher light intensity the photosynthetic activity of the sun-grown leaves already drops below the activity of shade-grown leaves (cf. JARVIS 1964), but in our opinion this may be one of the very reasons why in the third and fourth habitats of good light intensity this species is already left behind in the competition against the heliophyte *Quercus pubescens* (cf. LOGAN 1970).

In the investigated system, the light-leaf characteristic in the case of *Quercus pubescens*, prevails also in the lower leaves of the individuals grown in habitats of a higher light intensity, although these leaves are considered shade-leaves within their own foliage system.

The connection between the leaf anatomical characteristics and CO_2 assimilation ability of pre-adapted individuals living in different environmental conditions

It is known that the photosynthetic activity is primarily determined and influenced by the biochemical system of the photosynthetic apparatus. The adaptation to light conditions, for example, may manifest itself in the different activity of the enzyme carboxidismutase, within the chloroplast (BJÖRKMAN 1968). This enzyme is responsible for the coming into existence and quantity of the first products of photosynthetic CO_2 fixation. The quantitative differences of the leaf anatomical characteristics may also be considered an adaptation to the ecological conditions; the quantitative differences manifesting in these characteristics may be evaluated as the influence of the environmental factors affecting at the time of their formation (FEKETE—SZUJKÓ-LACZA 1973). The photosynthetic system in the young leaf is also under the influence of these effects. The very aim of our investigation was to discover the connection between the anatomical characteristics pointed out by us, and the capacity for CO_2 incorporation by the same leaves.

A parallel investigation of the anatomical characteristics and the photosynthetic activity is extremely difficult. The difficulties refer to both the selection of the characteristics to be measured and the optimal choice of the measuring conditions (e.g. that of inducing CO_2 assimilation). In the course

of an interpretation one must be aware of the fact that the actual cause-and-causality manifests itself only rarely on the surface (therefore it is nearly impossible to measure all the important, interplaying causes), hence one should attempt, by choosing an adequate method of assessment, to get to the core of the truer interconnections deep below the formal connection. In our opinion, path analysis our chosen method provides information on the non-mutual but cause-effect on the relationships between anatomical characteristics and CO_2 incorporation, and the rate of direct and indirect influences.

A great number of authors have dealt with the connections between the anatomy and photosynthetic activity of the canopy leaves. A considerable part of literature studies the question in connection with the functioning and openness of the stomata in experimental conditions. A second group of the works examines the influence of the two mesophyll layers on CO_2 assimilation. Some works deal with the gaseous volume of intercellulars within the mesophyll, and with the variation in CO_2 concentration, in connection with the functioning of stomata. It is only recently that attention is turning towards the connections between mesophyll cell dimensions and CO_2 assimilation (WILSON, COOPER 1967, etc.). The experimental character of works performed on the most diverse species, the conditions of the experimental set up render the adaptation of the results more difficult.

Dissimilarly to the available ecomorphological and ecophysiological works, we assess four anatomical characteristics in an identical investigational material. As regards their functions, these anatomical characteristics are very probably related to the various phases of CO_2 incorporation.

Behind the high correlation between the cell layer ratio examined in the mesophyll (palisade/spongy parenchyma ratio) and the CO_2 incorporation several indirect influences have their course upon assimilation (Table 9). The direct effect of the ratio of the two assimilating parenchymas is the lowest among the four factors examined (Table 8). It is noteworthy that in the connection between the other anatomical factors and the assimilation, the palisade/spongy parenchyma ratio plays, by its indirect effects, a fairly subordinate rate in all the three cases alike.

The statistical approach provides relatively little support as regards the role of the two assimilating layers in the photosynthesis. The ratio of the two layers mentioned are in general considered light adaptation, primarily the developmental size of the palisade parenchyma layer. STARZECKI (1962, 1967) attributes the major role to the spongy parenchyma in CO_2 assimilation, while a supporting-filtering role to the palisade parenchyma (cf. STARZECKI, TAIRBECKOV 1970). Other authors bring the two tissue layers and their ratio, and CO_2 assimilation respectively into relationship with the number and magnitude of the chloroplasts (ABEL 1956, IRMAK 1957); however, we have no observations of this character.

A fairly strong correlation manifested itself between the mesophyll chamber size and CO_2 incorporation (Tables 7, 10). Of the four factors the second has the greatest direct influence (Table 8). The influence of the mesophyll chambers upon the assimilation may be formulated so that the small chamber size is associated with a great chamber surface (in a unit of mesophyll space); the bundle sheath parenchyma constituting the chamber walls may influence the organic matter transport in a lateral direction (not considering possibly the crystal content of the bundle sheath parenchyma in vessels of the third and fourth grade — cf. FEKETE, SZUJKÓ-LACZA l. c.); while the dense network of vascular bundles guarantees the rapid conveyance of assimilates. On the other hand, in leaves with great mesophyll cells the rapid accumulation of the products may decelerate the formation of products containing nitrogen (Á. FALUDI-DÁNIEL ex. verb.). In addition to the direct influence of the chambers, there is a similarly negative indirect influence of probably another character through the intercellular size (Table 10).

The next two anatomical characteristics are in connection with CO_2 diffusion, and its control respectively.

The influence of the anatomical factors related to CO_2 diffusion is expressed by the incorporating ability and resistance against diffusion respectively. A satisfactory definition of these resistances, harmony between structure and function, is given by JARVIS (1971): "The resistances encountered by molecules of carbon dioxide in moving into the leaf from the source in the ambient air to the sink at the sites of reaction in the chloroplast may be used to describe quantitatively specific anatomical and physiological responses to environment which in many circumstances limit the rate at which photosynthesis proceeds."

An optimal CO_2 diffusion promotes and influences the utilization of especially high light intensities — at which also *Quercus pubescens* grows — rather than that of low light intensities.

The correlation between the intercellular ratio and CO_2 incorporation is fairly strong, and also the path coefficient value is the highest among all path coefficients (Tables 7 and 8). We believe that by this we succeeded in pointig out an anatomical factor able to influence the intensity of photosynthesis through controlling CO_2 supply.

The role of the intercellulars can be found in the fact that the free walls in contact with them constitute an incorporation surface in the gaseous exchange (TURRELL 1936, 1944). It was already LUNDEGÅRD (1922; cit. STÅLFELT 1960) who pointed out that the intercellular quotient deriving from the anatomical differences in the leaves influences the photosynthesis. He attributes an importance to the ratio between the cell surfaces bordering the intercellulars and the volume of the chloroplasts, for the favourable CO_2 diffusion. SIMONIS (1952) found, similarly to our results, high photosynthetic activity in

xerophytons grown in dry habitats, and he also suggests that the cause lies in the development of the internal/external surface ratio.

It is rather difficult to separate the influence of the intercellulars (intercellular resistance) from the stomatal resistance (JARVIS 1971); in such cases — in our opinion — the importance of the indirect approach increases.

So the intercellular ratio strongly influences CO_2 incorporation. High intercellular ratio and high photosynthetic activity can be pointed out in the leaves of individuals grown in the fourth habitat.

The drawing of the stomatal number into the investigation was justified by the fact that it had been demonstrated since long (e.g. by THODAY 1931) that the higher stomatal frequency of the xeromorphic leaves in certain species may accelerate CO_2 diffusion and assimilation. The stomatal number plays a part also as a resistance factor in the gaseous exchange; a greater stomatal number results in a lower stomatal resistance, as is known on the basis of measurements and calculation by BANGE (1953) and others.

In *Quercus pubescens* the value of the correlation coefficient between stomatal number and incorporated CO_2 is the smallest, while the direct influence of stomatal frequency is the third among the four anatomical characteristics examined (Tables 7 and 8). The direction of this influence is negative. The data are contradictory. The leaves of individuals obtained from the fourth habitat are of high stomatal frequency and of high ability to incorporate CO_2 (this, however, may be related to the intercellular ratio — a strong indirect influence —); the incorporation capacity of the leaves of individuals grown in the second habitat — which are also of high stomatal frequency — is at the same time low. Presumably, on the leaves of individuals developed at average light intensities differing according to the various habitats, also the stomata responded differently to the experimental light; the ratio of their opening is also a CO_2 diffusion, and thus an assimilation factor (cf. STÅLFELT 1935). According to HEATH and MEIDNER (1961) the opening and closing of stomata may show a close connection with water uptake. Our experimental conditions do not provide a possibility of determining this.

The correlation between stomatal number and photosynthesis is positive, in spite of its direct negative influence mentioned above; because of indirect effects (primarily owing to the influence through the intercellular ratio, mentioned above). So the influence of the intercellular ratio is noteworthy not only by its direct influence (Table 11).

If the condition of the site is now taken into consideration, we assume on the basis of data in the literature and also of our own preliminary investigations, that a higher light intensity increases, also by the strong openness of the stoma by day phases, the maximal utilization of CO_2 transport — in the leaves of hair oak in the third and fourth habitats, — and this may be better utilized by individuals of a higher photosynthetic capacity. Owing to the

higher light intensity also in the third and fourth habitats — as can be expected on the basis of investigations by BIERHUIZEN and SLATYER 1964, WHITEMANN and KOLLER 1968 — mesophyll resistance against CO_2 diffusion may also decrease, so this effect may add to the former. On the other hand through the earlier closing of the stomata (cf. POLSTER, WEISE, NEUWIRTH 1960) the secondary effects of high light in connection with water loss check indirectly, in time, the actual utilization of this higher capacity (decrease in production duration, especially in the fourth habitat).

The contradiction existing between the assimilation capacity of the leaves of the sample trees (Table 1) and the actual remaining production (Table 4) may be solved by the water factor — varying water supply and water economy in the habitats. — It is clear that this production is somewhat independent of the capacity of CO_2 assimilation (the direction of the correlation is directly negative, NS). Within identical light levels the wood mass values in habitats with good water supply surpass four times those measured in habitats with unsatisfactory water supply. So in the various habitats the shortage in water strongly controls the *Quercus pubescens* leaf in its utilization of the photosynthetic-assimilatory capacity determined biochemically and anatomically. This fact calls attention to the necessity of further investigations directed towards the course of activity in time.

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NEW GYMNOSPERMS FROM THE TRIASSIC (GONDWANA) BEDS OF TIKI, MADHYA PRADESH, INDIA

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The paper describes fossil Gymnosperms woods, assigned to the new genus *Tikioxylon*, collected from Triassic beds of Tiki, South Rewa, Gondwana Basin. *Tikioxylon* is characterized by the spiral thickenings and araucarian pitting on the walls of tracheids. Two species viz. *T. hughesii* and *T. spiralli* are also enumerated showing differences in growth rings, cross field pits and medullary rays.

Introduction

The Tiki beds (23, 56: 81, 22) in South Rewa, Gondwana Basin, are now referred to the upper Triassic (KRISHAN, 1956). Ever since T. H. HUGHES discovered them in 1881, only a silicified wood, *Mesembrioxylon malerianum*, was described by SAHNI (1931). Abundant fossil logs have been known to exist in Tiki beds (KRISHNAN, 1956), and systematic study, in progress, has revealed them to be Gymnosperms. The Tiki beds contain standstones (white green and rubby, usually calcareous) and red green clays. Numerous fossil woods have been collected during May-June 1966—69; about 3–4 miles South of Tiki. The present paper is based on 22 fossil woods, ranging from 6 cm to 68 cm in size. The woods were sectioned at the Birbal Sahni Institute of Palaeobotany, Lucknow. Certain pieces were macerated subsequently, to reveal spirals on the walls of tracheids, which are under detailed investigation.

Description

Tikioxylon n. gen.

(Specimen No. T2/1—21 GOSWAMI Collections.)

The description of the new genus is based on woods ranging from 6 cm to 68 cm in size. The woods are chocolate to dark brown in colour and vary in dimensions (Plate IA). The preservation of some of the woods is very fine.

Tikioxylon is characterized by the spiral thickenings on the walls of tracheids with typical araucarian pitting. The resin canals or ducts are absent. Beside these constant features, the woods differ in minute details and therefore considered as two species.

I. Tikioxylon hughesii n. sp.

[Specimen No. T2/1—13 the wood comprises piece sof logs (Plate I, A) of dark brown colour.]

Growth rings, indistinct, xylem parenchyma and resin canals absent.

Tracheids — long and wavy, oval and round in cross section (Plate I, B) rarely pentagonal, ranging from 24—42.5 μ in diam. Tangential walls scarcely pitted. Pits uniseriate and compressed 12—18 μ in diam. Radial pits round (Plate I, C, D) to hexagonal 17.7 μ—27 μ in diam. Both uniseriate and biseriate compressed pits show circular pores. Spiral thickening (Plate I, E) prevalent on both sides. Two spirals often lie parallel to each other and enclose the pits (Fig. 1). Due to additional mineral deposition (iron pyrites) at some places, they tend to thicken. The inclination of these spirals against the wall of the tracheids is 20—60°. Both clockwise and anti-clockwise spirals occur in the same tracheids. At certain places, very thick spirals enclose the biseriate pit (Fig. 2) which are comparatively smaller in size. At still other places, the spirals form networks (Plate I, F, G) which, however, never enclosed the pits.

Cross field pits - generally compact and close, rarely separate with circular pores (Fig. 3). Maximum number of cross fields in a cross field not exceeding six.

Medullary rays — not visible to the naked eye; simple, homogeneous often uniseriate (85%) occasionally biseriate (Fig. 4; 14.9%) and rarely triseriate (partly, 0.1%; 2—10 cells thick and 1—34 cells high. The average diameter of ray cells [in 50] is 23.4 μ).

II. Tikioxylon spiralli n. sp.

(Specimen No. T1, 1—5; T4, 1—4.)

Nine pieces of fossil logs, one 68 cm long (Plate II, A). Growth rings distinct (Plate II, B) 245 to 1200 μ apart, showing transition from spring to summer wood. Spring wood generally wide, consisting of large tracheids 16 to 61 μ in diam., moderately thick-walled, circular to pentagonal with open and wide lumina. Summer wood composed of thick-walled, squarish, rectangular or rounded tracheids with narrow lumen of 12 to 51 μ in diam. (Plate II, B). xylem rays simple, homogeneous, mostly uniseriate, rarely biseriate (Plate II, C; Fig. 5). Rays 2—10 cells thick and 1—16 cells high, diameter of ray cells varying between 13—28 μ (average 21 μ). In radial section, ray cells rectangular and unpitted, tangential walls vertical, curved or slanting in position and also smooth and unpitted.

The cross field pits (Fig. 6) are 1—5 in number, bordered or scattered, singly or arranged in twos (side by side), mostly circular, of two sizes. Smaller pits ranging 9—12.4 μ, bigger ones 14—25 μ in diam., pores generally circular, rarely obliquely lenticular.
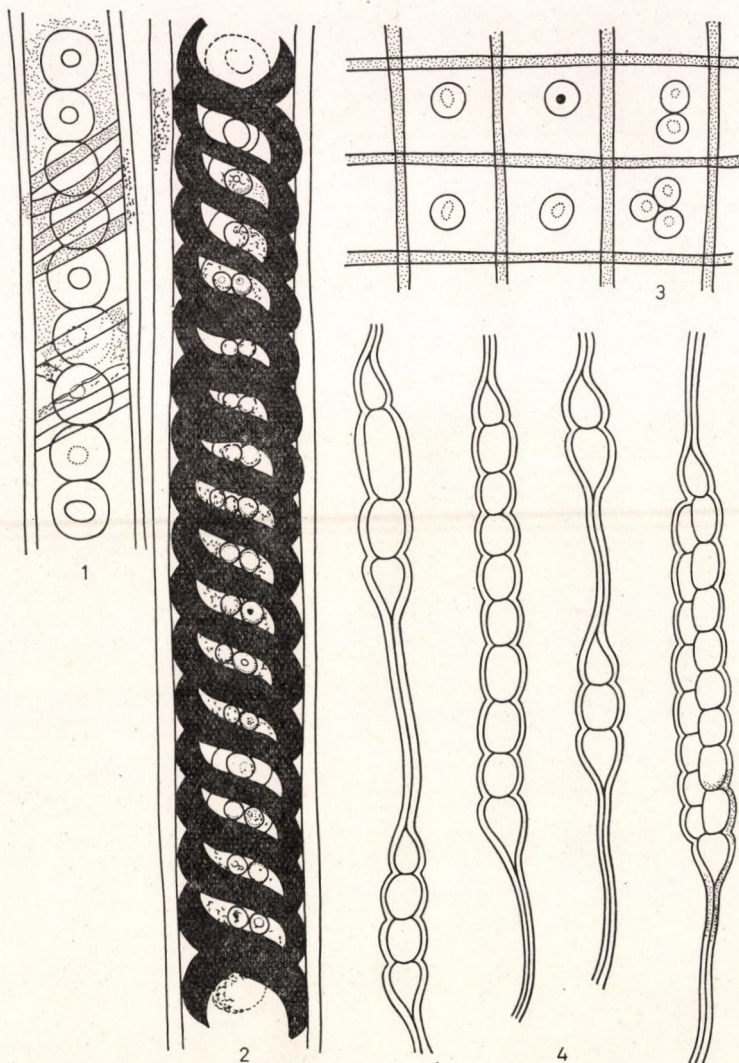
Fig. 1. Tracheid in radial view showing uniseriate pits with intervening spirals (T2—3, ×625)
Fig. 2. Tracheid in radial view showing a highly thickened spiral owing to deposition of iron pyrite. Pit pore is rather well preserved. Complete pit is also seen. At some places, decay of the pit is represented by a clustering of "micro-pits" (T2—3, ×800)
Fig. 3. 1—3 Cross field pits (T2—4, ×625)
Fig. 4. Tangential section showing uniseriate and biseriate medullary rays (T2—5, ×625)

Pitting on radial walls of tracheids often uniseriate (Fig. 7), rarely biseriate (Plate II, D; Fig. 8), pits often circular, oblique due to compression, pores circular or obliquely placed, ranging 3—5 μ diam. Smaller pits, ranging 5–9.4 μ diam., also observable. Tangential pits less frequent.

Spiral bands (Plate II, C and E) on tangential walls of tracheids 1–2.9 μ
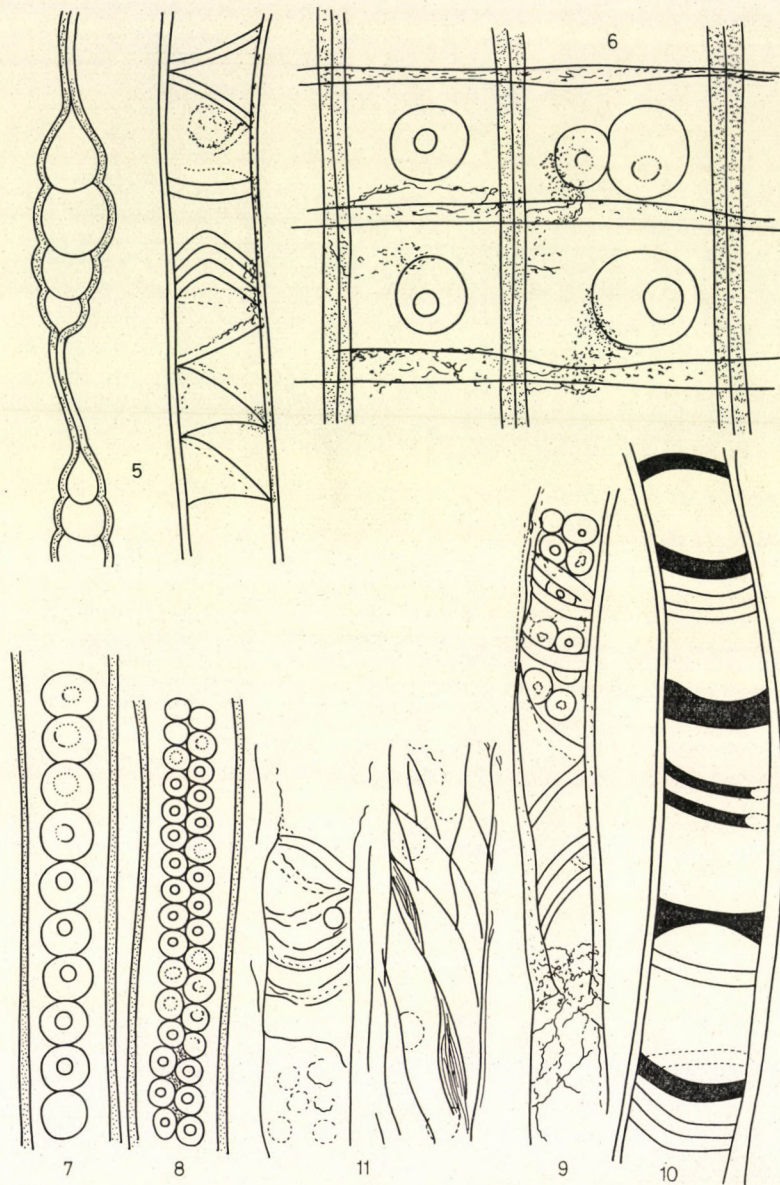
Fig. 5. Tangential section showing uniseriate medullary ray and irregular spirals on the Tracheid (T1—2, ×625)

Fig. 6. Cross field pits 1—2 accompanied by mineral deposition (T1—3, ×800)

Figs. 7, 8. Uniseriate and biseriate pitting on the radial walls of tracheid (T1—4, ×625)

Fig. 9. Tracheid in radial plane in ***Tikioxylon spirallii*** showing spirals at a very close ascend. Lower portion of the tracheid shows decay of the pits and spirals forming "network" (T1—4, ×625)

Fig. 10. Tracheid in radial section of ***T. hughesii*** showing irregular spirals appearing like annular bands (T2—5, ×800)

Fig. 11. Tracheids in tangential section of ***T. hughesii*** showing typical spirals and decay of both spirals and pits, thus forming network (T2—5, ×800)

thick, mostly uniseriate, rarely biseriate (Text Fig. 5). Radial sections showing typical spirals along with uniseriate meduallary rays (Figs 9, 10). Sometimes bands too close, giving an illusion of an annular thickening (Figs 9—10). Bands sometimes passing across the pits or through the space between the separate pits. Spirals forming network absent.

Discussion

Comparison with living woods

Spiral thickenings occur in the *Taxales* and in *Pseudotsuga*, *Picea* and *Larix*, but the members of *Pinaceae* can be eliminated, as the present woods show neither resin ducts nor abietinean pitting (Greguss, 1955).

The spirals on the walls of tracheids, especially in *Tikioxylon spiralli* (Plate II, C, E; Fig. 9) and *T. hughesii* (Fig. 10), recall *Taxus baccatta* L. in which the spirals ascend sometimes in very low angles causing the spirals to appear as an almost horizontal annular thickening. In addition to spirals, *Taxus canadensis* Marshal also shows (see Greguss 1955, Plate 81, Fig. 3) a single pit in the cross field.

The outstanding feature, however, of the araucarian pitting in the present woods, along with the spiral bands, eliminate a comparison with any living Gymnospermous wood. Comparison with fossil woods: Even among fossils, there are only a few woods which can be drawn into comparison within reason. Woods with spirally thickened tracheids are as old as the Permo-Carboniferous. *Tyxopitys* was first described by Kräusel from the Permian of S–W Africa and is considered a member of the Lower Carboniferous flora of Siberia (Shilkina, 1960), while *Prototaxoxylon* (kräusel–dolianiti) and *Paratax-xopitys* Maniero (Kräusel–Dolianiti, 1958) come from the Brazilian Permian. The wood of *Brachyphyllum spiroxylum* (Bose, 1952) from the Indian Jurrasic and *Prototaxoxylon intertappeum* (Prakash-srivastava 1961) show araucariod (?cordaitean) pitting on the tracheids. The latter wood also shows spiral bands, but dissimilar to the present woods. It differs in many details. In *Protaxoxylon intertrappeum*, there are unlike the present wood, spaces between the pits (Prakash – Srivastava, 1961, Plate I; Figs 4, 11, 16 and 18), thin spiral bands pass through the pit pores, the pit pores may be lenticular and some places, rims of Sanio appear to be present. The present material also differs in the structure of the medullary rays and the number of pits per cross field. Fossil woods of the genus *Taxoxylon* Unger also possess true spiral thickenings, but show the abietinean type of pitting in the tracheids, similar to those found in the living genera of the family *Taxineae*. Kräusel indicated that (hardly few) some of fossil woods described as *Taxoxylon* really belonged to *Taxaceae*. Since the genus *Taxoxylon* also included woods with resin ducts,

KRÄUSEL and JAIN (1963) invalidating this generic name, proposed *Taxaceoxylon* to accommodate woods with spiral thickenings and having no resin ducts. Therefore, a wood similar to *Taxoxylon rajmahalense*, Bhardwaj, from the same age, they named as *Taxaceoxylon* sp. f. *rajmahalense* (Bhardwaj) KRÄUSEL and JAIN.

The present woods assigned to *Tikioxylon* come from the Upper Triassic. Although the oldest Taxad, *Palaeotaxus rediviva* Nathorst (see KRÄUSEL and JAIN, 1963), is reported from the Upper Triassic, these woods, including *Taxaceoxylon*, never showed araucaroid pits.

In contrast to this, the pitting in the present woods corresponds more closely to the pits seen in species of *Araucarioxylon* (OGURA, 1960, and personal communication). However, of the almost two dozen species described as *Dadoxylon* (= *Araucarioxylon*, see KRÄUSEL et al., 1961; SAH and JAIN, 1963; SURANGE and MAITHY, 1962 and MAHESWARI, 1964), no wood has ever shown any spiral thickening on the tracheids.

The features met in *Tikioxylon* are incomparable to any living or fossil gymnospermous plants. This new genus comprises two species:

T. hughesii, dedicated to T. H. HUGHES, the discoverer of the Tiki beds differs, with *T. spiralli*, in having no growth rings, the spiral thickening forming a network (probably due to decay of the pits), the minimum number of cross field pits per cross field being 2, and in having higher medullary rays.

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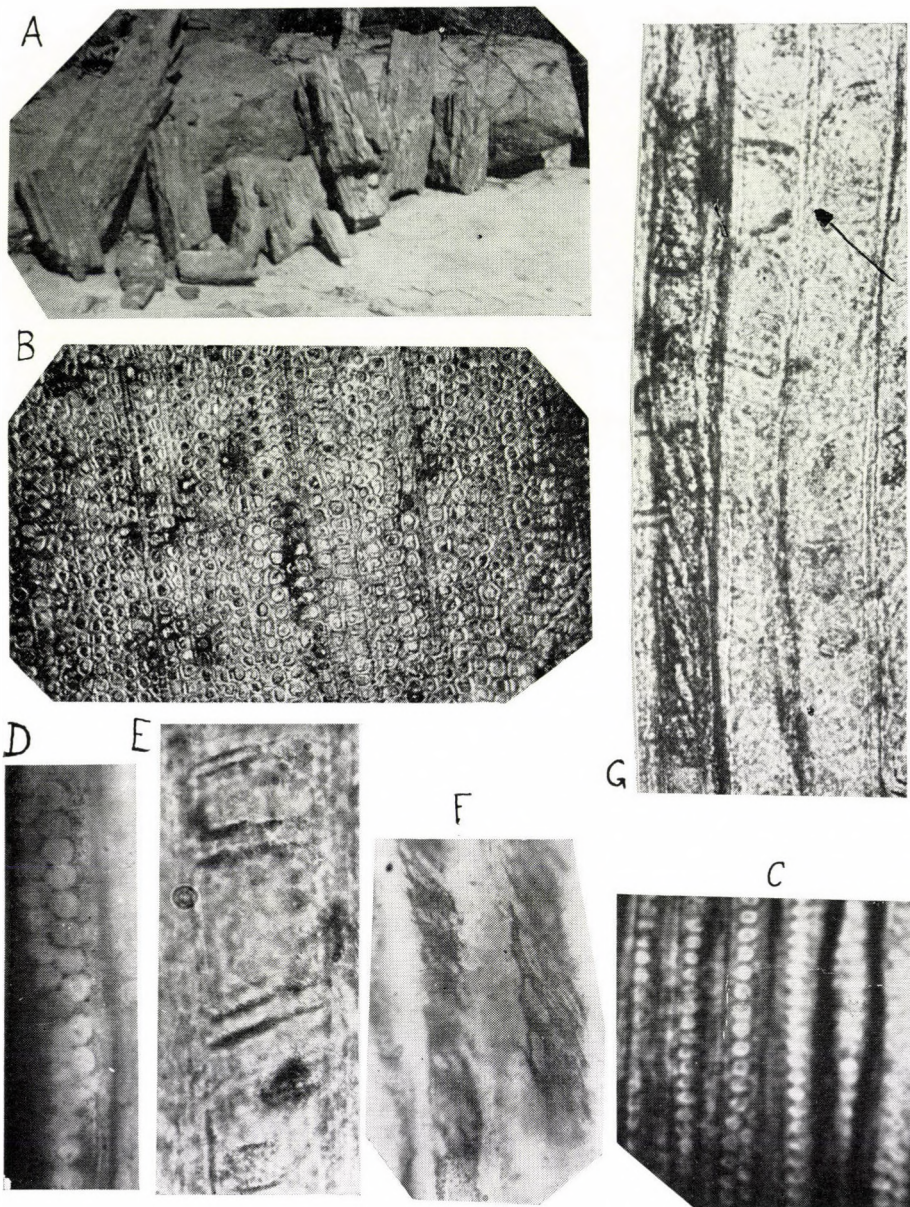
Plate I

Fig. A. Fossil logs of *Tikioxylon* gen. nov. of varying sizes (×1/10)
Fig. B. Cross-section of *T. hughesii* sp. nov. showing no growth rings (T2, ×75)
Fig. C. Radial walls of tracheids showing uniseriate and biseriate pits (T2—4, ×150)
Fig. D. A tracheid in radial plane showing biseriate, alternate, compressed pits (×150)
Fig. E. Spiral thickening on radial wall of tracheid (T2—3, ×500)
Fig. F, G. Spirals forming networks; probably both are formed owing to decay of the pits and spirals. In Fig. G irregular spirals are seen in adjacent tracheids (T2—4, ×450)
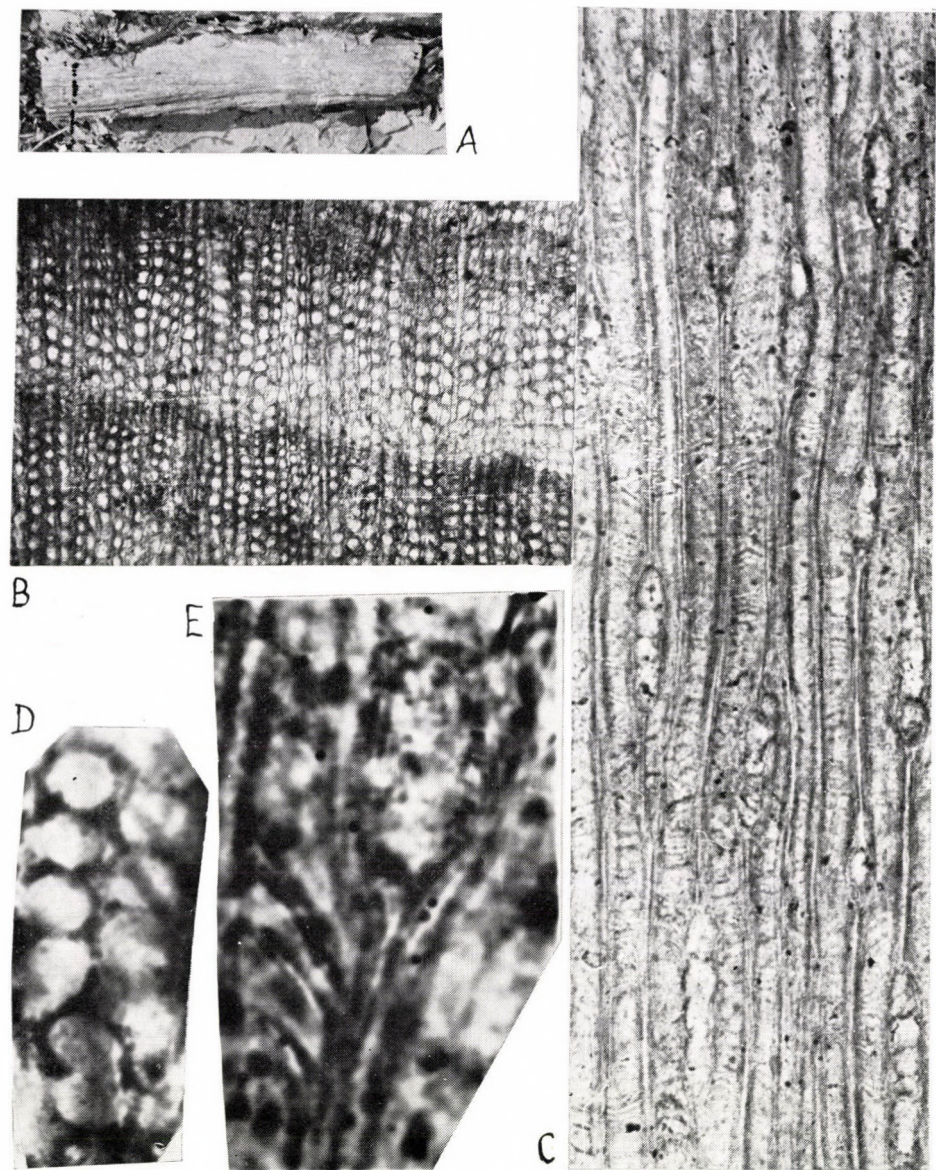
Plate II

Fig. A. Fossil log relegable to *Tikioxylon spiralli* (poor preservation) ×1/10
Fig. B. Cross-section of *T. spiralli* showing well-marked growth rings (T1—3, ×75)
Fig. C. Portion of a tangential section showing spirals on the tracheids and uniseriate medullary rays (T—1, ×150)
Fig. D. Biseriate alternate pits on radial wall of a tracheid (T1—4, ×500)
Fig. E. Enlarged portion of a tangential section showing parallel spiral bands on a tracheid, with half a medullary ray (T1—4, ×500)

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INVESTIGATION AT THE EARLY STAGE OF EMBRYOGENESIS INTO THE DEVELOPMENT OF THE ADVENTIVE EMBRYO ORGANIZED FROM A CELL OF THE CALLUS TISSUE IN DAUCUS CAROTA L.

By

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The adventive embryogenesis in the callus tissue culture of *Daucus carota* L., placed on RM-1964 nutrient medium, supplemented with 0.02 and 1.00 ppm kinetin and 2 ppm IAA, was examined. According to observations, the embryogenesis of embryoids developing from the differentiated callus cells is in agreement, also in the pro-embryonic state of a few cells, with the development of embryos developing from the zygote.

Introduction

Adventive embryos could be induced from the tissue culture of various plant species (REINERT 1968, WARDLAV 1968, STEWARD 1969). However, the ontogenesis of these embryos could not be observed directly (KATO 1968). Embryogenesis could be reconstructed only from the various developmental stages in the cases of both the somatic cultures (REINERT 1959, STEWARD 1963, KATO—TAKEUCHI 1963, HALPERIN—WETHERELL 1964, VASIL—HILDEBRANDT 1965), and the haploid cultures (GUHA—MAHESHWARY 1967, NITSCH—NITSCH 1969, HESZKY 1971).

Closer results were attained from the observation of embryoids organized from explantates with several cells, and cell groups (KONAR—NATARAJA 1965, HALPERIN—JENSEN 1967, KATO 1968). BACKS—HÜSEMANN—REINERT (1970) were among the first to report on the direct observation of adventive embriogenesis in the one-celled culture of carrot. However, the observation of the development of the proembryos with a few (2—20) cells could not be carried out by the applied technique of cell culture. These early phases of embryogenesis can be examined only in separate preparations. The results of these investigations are described in the present paper.

Material and methods

The basic nutrient medium (RM-1964, LINSMAIER—SKOOG 1965) was completed with 2.00 ppm IAA and 0.02 and 1.00 ppm kinetin the undifferentiated root callus tissue of the Russian carrot variety called "Wesraya vennaya", was placed on this substrate. The cultures were maintained at natural light supplemented with, artificial light (flourescence lamp) at a

temperature of +25°C. Beginning with the second week after isolation, the various phases of embryogenesis were examined in stained preparation. The pictures were taken on NP 20 film, with an MOM photo complement mounted on a "Laboval" Zeiss microscope (10—40 × objective, 2.5—6.3 × projective).

Results and discussion

The following observations were made in the course of cytological investigations of the isolated callus tissue. The differentiated callus cells (Fig. 1/A) transversally divide into two, and the two-celled proembryo comes into existence (Fig. 1/B). The initial cell of the proembryo suspensor — with a transversal wall — divides into a basal cell and a suspensor cell which continues dividing (Fig. 1/C). On the other hand, the apical cell of the proembryo, by dividing longitudinally, creates two descendent cells. In this way the fourcelled proembryo forms a lying T-shape (Fig. 1/D). The two terminal cells form quadrants with a transversal wall (Fig. 1/E), then an octans with a periclinal wall (Fig. 1/F). Subsequently each cell divides periclinally and as a consequence a peripheral and a central meristema region separate in the proembryo (Fig. 1/G).

As a result of the gradual organization of the developing embryo, first the multicellular globular stage (Fig. 1/H—I), then the heart-stage can be observed (Fig. 1/J). On the embryo that has become polar, the radicle differentiates towards the suspensor, while on the opposite pole the cotyledon begins to differentiate. The elongation of the radicle and hypocotyl fundaments resulted in embryos of torpedo stage already 4—5 week after the isolation (Fig. 1/K). Following this stadium, the development of the cotyledon stagnated — similarly to the results obtained with in vitro embryo cultures — but in the ripe embryos, formed after a further development and maturing, the procambial bundle sheath fundaments can be distinguished well (Fig. 1/L).

In the last analysis it can be stated that the adventive embryo development is in agreement even in its few-celled proembryo state with the embryogenesis of the embryo developing from the zygote.

Acknowledgement

I should like to express my gratitude also in this place to Professor M. Maróti for his useful advice in the elaboration of the subject.

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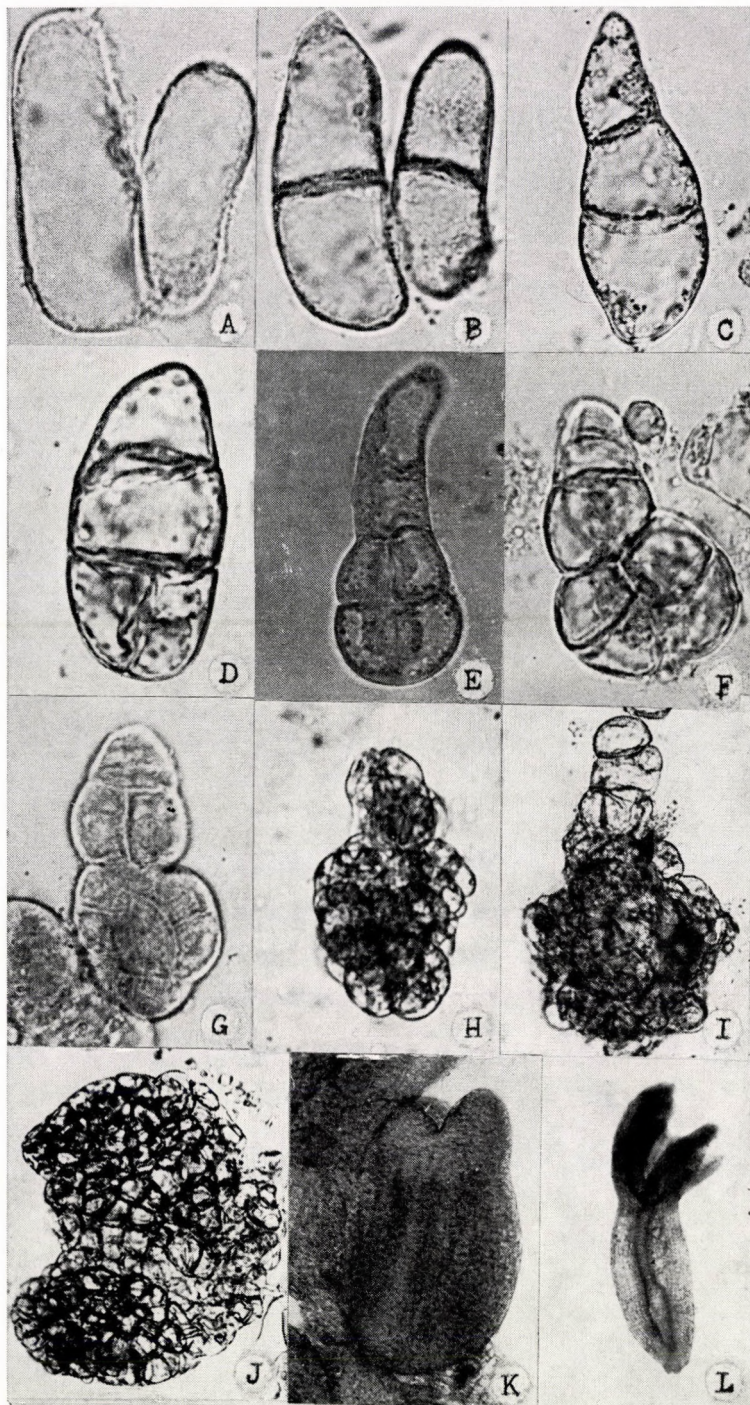
Fig. 1/A. Callus cells turned embryonic (40 × obj., 6.3 × proj.)
Fig. 1/B. Two-celled proembryo (40 × obj., 6.3 × proj.)
Fig. 1/C. Three-celled proembryo (40 × obj., 6.3 × proj.)
Fig. 1/D. T-shaped proembryo (40 × obj., 6.3 × proj.)
Fig. 1/E. Four-celled embryo initial primordium (40 × obj., 6.3 × proj.)
Fig. 1/F. Eight-celled embryo initial primordium (40 × obj., 4 × proj.)
Fig. 1/G. Separation of central and peripheral meristem primordia (40 × obj., 4 × proj.)
Fig. 1/H—I. Globular stage embryo (20 × obj., 2.5 × proj.)
Fig. 1/J. Heart-stage embryo (10 × obj., 4 × proj.)
Fig. 1/K. Embryo in torpedo stage (10 × obj., 2.5 × proj.)
Fig. 1/L. Developed embryo (10 × obj., 2.5 × proj.)

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ULTRASTRUCTURE EXAMINATION OF FOSSIL PTERIDOPHYTA SPORES AND GYMNOSPERMATOPHYTA POLLENS

By

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Ultrastructure examinations were carried out on fossil *Pteridophyta* spores and *Gymnospermatophyta* pollen grains. In the course of our work we came to the following results: No well-definable layers on the ultrastructure of the spore wall of the Lower Eocene and Upper Cretaceous isosporous ferns [*Leiotriletes adriennis* asp. *triplanoid*, *Toroisporis* (*Toroisporis*) *eocenius*, *Appendicisporites tricuspidatus*, *Microfoveolatosporis pseudodentatus*] can be distinghuished. Two main layers can be separated (ectexosporium and endexosporium) on the exosporium primarily through electron affinity. On the Jurassic *Spheripollenites scabratus* an exine ultrastructure of the Angiospermatophyte type could be determined. The finer structure of the wall of the Upper Cretaceous cf. *Araucariacites* v. *Granulatisporites* fsp. is of an Angiospermid character. The form genera *Classopollis* and *Classoidites* can be well distinguished with the ultrastructure of the columella layer above the endexine.

Introduction

In the previous studies (KEDVES and PÁRDUTZ 1970a, b; HEGEDÜS, KEDVES and PÁRDUTZ 1971; KEDVES, HEGEDÜS and PÁRDUTZ 1971; HEGEDÜS, KEDVES and PÁRDUTZ 1972; KEDVES and PÁRDUTZ 1972, 1973) the results obtained in the ultrastructure investigations of Eocene and Upper Cretaceous Angiospermatophyte pollen grains were given. We propose to continue the ultrastructural examination of fossil Angiospermatophyte exines, but also consider a similar examination of Pteridophyte — primarily *Filicales* — and Gymnospermatophyte microfossiles. The problem that has emerged is to what extent can a correlation be established between the fossil Pteridophyte spores, and the Gymnospermatophyte and Angiospermatophyte pollen grains on the basis of the submicroscopic structure?

Concerning information on the ultrastructure of fossil and recent spores and Gymnospermatophyte pollen grains, PETTITT's work (1966) is fundamental, despite the fact that data on the ultrastructure of recent spores can be found also in earlier papers (e.g. AFZELIUS, ERDTMAN and SJÖSTRAND 1954, AFZELIUS 1956, ERDTMAN 1956). Subsequent results obtained on the spores of recent and fossil heterosporous ferns are also significant (KEMPF 1969a, b, 1971). The inference drawn by PETTITT and CHALONER (1966) on the basis of ultrastruc-

tural data on *Classopollis* type pollen grains must also be mentioned here: "La structure de l'exine se révèle aussi caractéristique que la morphologie du grain entier et sa complexité n'est pas dépassée, même par les Angiospermes actuelles."

Material and method

The sporomorphs investigated ultrastructurally are as follows:
1. *Leiotriletes adriennis* (R. Pot. et Gell. 1933) W. Kr. 1959 asp. *triplanoid* Kds. 1961 (1 in Plate I). Locality: Zirc (Hungary), Lower Eocene, black, slightly sandy clay layer.
2. *Toroisporis (Toroisporis) eocenicus* Kds. 1966 (Figs. 1, 2, Plate II). Locality: Zirc (Hungary), Lower Eocene, black, slightly sandy clay layer.
3. *Appendicisporites tricuspidatus* Weyl. et Greif. 1953 (Fig. 1, Plate III). Locality: Herend (Hungary), Upper Cretaceous coal layers.
4. *Microfoveolatosporis pseudodentatus* W. Kr. 1959 (1. 2 in Plate IV). Locality: Zirc (Hungary), Lower Eocene, black, slightly sandy clay layer.
5. Cf. *Araucariacites* v. *Granulatisporites* fsp. (1 in Plate V). Locality: Herend (Hungary), Upper Cretaceous coal layers.
6. *Spheripollenites scabratus* Couper 1958 (1 and 2 in Plate VI). Locality: Urkut, Jurassic carbonate manganese ore.
7. *Classoidites glandis* Amerom 1965 (1 in Plate VII). Locality: Aveiro (Portugal). Upper Cretaceous, coaly, clayey layers.

For the detailed description of the method applied in the investigations see the work of KEDVES and PÁRDUTZ (1970b).

Results and discussion

1. *Leiotriletes adriennis* (R. Pot. et Gell. 1933) W. Kr. 1959 asp. *triplanoid* Kds. 1961 (Figs 2—4, Plate I)

No well-definable layers on the spore wall can be distinguished even with the TEM method. On the basis of the electron affinity, a thicker external and a thinner internal layer (about one-third of the former) can be established (Fig. 4, Plate I). As a consequence of the triplanoid form, we obtained data also on the ultrastructure of the laesura in our ultra-thin sections (Figs 2, 3, Plate I). The "extragerminal" spore wall is interrupted along the laesuras, the highly attenuating part of the external wall covers the laesuras (2 in Plate II).

On the basis of the optical microscopic data, the examined spore is a remnant of the genus *Lygodium* in the family *Schizaeaceae*, thus it is an isospore. The ultrastructure of its spore wall substantially deviates from that of the Angiospermatophyte exines, so it is more appropriate to use the expression exosporium than to call it an exine, and to call the two layers, separating by the electron affinity, ectexosporium and endexosporium, respectively.

2. *Toroisporis* (*Toroisporis*) *eocenicus* Kds. 1966 (Figs 3, 4, Plate II).

Similarly to the former spore, layers can be separated only on the basis of electron affinity. There is a thicker ectexosporium and a thinner endexosporium also in this form-species (Fig. 4, Plate II). A difference can be estab-

lished only on the external wall, where the ectexosporium under the surface is of a stronger electron affinity (Figs 3, 4, Plate II). Thus two parts can be separated on the ectexosporium (that is, ectexosporia A and B); it must, however, be emphasized that this separation may be also a secondary phenomenon, having come into existence owing to fossilization. The fourth picture of Plate II illustrates the ultrastructure of the torus.

The form-species is a remnant of a plant belonging to the family *Gleicheniaceae*, and also an isospore.

3. *Appendicisporites tricuspidatus* Weyl. and Greif. 1953 (Figs 2, 3, Plate III)

A fairly characteristic *Schizaeaceae* spore of the Upper Cretaceous, within the *Normapolles* region, probably an isospore. On the basis of an inference by Góczán (1964), this form-species is significant also from the point of view of fine stratigraphy. Its exosporium divides also into ectexosporium and endexosporium. One of the fairly characteristic sculpture types of the genera *Anemia* and *Mohria*, the canaliculate, is well observable also in this spore-species (Figs 2, 3, Plate III). The result is essential, because in this case it is solely the ectexosporium which takes part in the formation of the sculpture; the endexosporium is of identical thickness under both the striae andmuri (Fig. 3, Plate III).

4. *Microfoveolatosporis pseudodentatus* W. Kr. 1959 (Figs 3, 4, Plate IV)

On the basis of the optical microscopic examinations by Kedves (1961) this spore represents the family *Psilotaceae* also in the European Lower Tertiary deposits. This spore is a good subject for investigations, from several points of view, concerning the other main type — the monolete spores — after the trilete spores investigated ultrastructurally above.

The ultrastructure of the spore wall in the recent *Psilotum nudum* Griseb. is known on the basis of Pettitt's work (1966). He examined acetolyzed spore walls stained with lead hydroxide. On the basis of his figures, the wall is generally uniform, but by the electron affinity two layers can be recognized; however, probably because of the means of fixation the electron affinity of the internal layer is stronger than that of the external one. About half of the exosporium takes part in the formation of the surface ornamentation (Fig. 3, Plate 11; Bull. B. M. (N. H.) Geol. 13. 4).

The surface ornamentation extends the about 1/4 the whole thickness of the spore wall. The division into two layers is not expressed in our sections, which may be due to their poor quality, or to the secundary changes incurred during fossilization (Fig. 3, Plate IV).

Figure 4, Plate IV, illustrates the longitudinal section of the spore apex and the laesura. In superior view of the laesura, the exosporium is interrupted conspicuously but a thin wall section covers it (x); this may be the outermost "covering" layer of the ectexosporium, securely determinable, however, in cross-sections only.

5. Cf. *Araucariacites* v. *Granulatisporites* fsp. (Figs 2—4, Plate V)

The form, examinated by optical microscope, resembles the genus *Araucariacites* Cookson, 1947, although a Y-shaped tetrade scar, or a formation similar to it, appears on the examined specimen. So this sporomorph is uncertain from this point of view.

The cause of our discussing also this datum is that the ultrastructure of this form best resembles the ultrastructure of the "angiospermid" exine. The external layer is an expressed tectum, bearing projecting ornamental elements of varying form and size (Figs 3, 4, Plate V). Under the tectum, there is a well-definable columella layer with elements of varying form, whose approximately tangential section shows a meshed structure (Fig. 2, Plate V). No foot layer can be recognized under the columella layer.

This ultrastructure is sharply separable from the isosporous ferns discussed above but owing to the lack of foot layer it cannot be wholly identified with the Angiospermatophyte exines. It also separates from the ultrastructure of recent Gymnospermatophyte taxa known from literature so far. Therefore, assumably, we are dealing here with an ancient heterosporus Pteridophyte microspore, or with an extinct Gymnospermatophyte pollen, from which more developed types or possibly Gymnospermatophyte or Angiospermatophyte of a higher order have arisen. Taking into consideration the geological age of the relic, the Upper Cretaceous — of a decisive importance in the formation of the new floral types — the presence of this problematic and transitional type may be taken as natural. These sporomorphs, less characteristic also light microscopically, are worthy of further through investigations.

6. *Spheripollenites scabratus* Couper 1958 (3—6 in Plate VI)

The ultra-thin sections were obtained from two, still unseparated specimens of a tetrad (Figs 1, 2, Plate IV). The exine consists only of a tectate and imperforate ectexine. The surface of the tectum is covered with fine and densely spaced projections resembling papillae. The columella layer consists of radially oriented columnar elements; the thickness of the layer largely agrees with that of the tectum. There is a thin foot layer underneath (Figs 3—6, Plate VI).

The ectexine ultrastructure basically agrees with the Angiospermatophyte exines.

On the basis of its optical microscopic morphology, COUPER (1958) correlated the form-species conditionally to the *Taxaceae*. Comparing GULLVAG's (1966) data on the ultrastructure of recent Gymnospermatophyte pollen grains — among them those of *Taxus baccata* L. f. *elegantissima* — and PETTIT's (1966) on *Taxus baccata* L., with our own results, one has to infer that, with respect to ultrastructure, *Spheripollenites scabratus* Couper, 1958, cannot in any case be connected phylogenetically with the recent inaperturate Gymno-

spermatophyte pollen grains. It is probably one of the representatives of the ancient Angispermatophyte type in the Jurassic.

7. *Classoidites glandis* Amerom 1965 (Figs 2—4, Plate VII)

With the electron microscopic method five layers can be separated on the exine. The ectexine divides into four layers, with the endexine beneath. The surface of the outermost layer (tectum) is uneven, ornamented sporadically with spinae and transversed with narrow channels (1). There is an extremely thin columella layer below it (2); the following layer is about twice as thick as the tectum (3). The next broad layer consists of various globular, ellipsoid, frequently anastomozing ultrastructural elements resembling the columella layer of angiospermous pollen grains (4). The elements of this layer do not unite on their basis, no newer foot layer develops, and there is a thick endexine of lamellar ultrastructure directly beneath it.

PETTITT'S and CHALONER (1964) separated also five layers on the exine of *Classopollis*. Proceeding inwards, the various layers were named tegillum (1), columellae (2), ectonexine$_1$ (3), ectonexine$_2$ (4), and endexine (5). Our genus deviates from the fine morphology of *Classopollis* in the perforated tectum, but especially in the fine morphology of the fourth layer. In *Classopollis*, it consists of columnar elements of a more or less radial direction. This feature separates the two genera well and it also corroborates the optical microscopic differences. Namely, this layer shows the optical microscopically characteristic striate exine, of *Classopollis* and the granular exine of *Classoidites*. In the possession of the ultrastructural data, these are obviously intratectate elements. AMEROM (1965) wrote, when describing *Classoidites glandis* that the exine is probably tectate where the columella layer forms a reticulate pattern, especially at the equatorial part.

As has been stated by PETTITT and CHALONER (1964), the ultrastructure of the *Classopollis* exine exceeds in its intricacy even that of the angiospermous pollen grains. This has already been supported by the results obtained on several ultrastructures of the examined fossil angiosperm pollen exines (KEDVES and PÁRDUTZ 1970a, b; HEGEDÜS, KEDVES and PÁRDUTZ 1971). As against the general triplate ectexine division of the Angiosperms (tectum, columella layer foot layer), we suggest the following possibilities for the interpretation of the layers established in *Classopollis* and *Classoidites*.

If we consider layers 1—3 a subdivided tectum, then there is no foot layer beneath the columella layer, only the endexine with of thick lamellar ultrastructure. The foot layer can be interpreted as a tangentional ectexine layer above the endexine. In this case it resembles in essence the form-genus *Wodehouseia* (LEFFINGWELL, LARSON and VALENCIA 1970).

Since in the fossil angiospermous pollen grains examined so far the triple division of the ectexine is general, the possibility may be suggested that there is a connection between the exine ultrastructures of the *Classopollis* and

Wodehouseia types. Both agree in the endexine being developed, without a foot layer but with a characteristic columella layer above it. So the possibility arises that *Wodehouseia* might be the pollen of an Gymnosperm, or that *Classopollis* and *Classoidites* are ancient Angiosperms; nor is it precluded that during the evolutionary process these pollen grains represented a stage between the Gymnosperms and Angiosperms taken in the modern sense. No final decision of the question is possible at present; however, we consider it necessary to separate the exine ultrastructures of the *Classopollis* and *Wodehouseia* types from those of the other fossil Angiosperms.

Conclusions

1. No connection can be established between the ultrastructure of the spore wall in the isosporous *Pteridophyta* from the Upper Cretaceous and the Lower Eocene and the exine ultrastructure of the Angiospermatophyte pollen grains.

2. The Angiospermous character is recognizable on the exine ultrastructure of the inaperturate forms from the Jurassic and the Upper Cretaceous.

3. The exine ultrastructures of the *Classopollis* and *Wodehouseia* types should be separated from the other fossil Angiosperms.

Summary

No well-definable layers can be determined on the ultrastructure of the wall in isosporous ferns. (*Leiotriletes adriennis* asp. *triplanoid*, *Toroisporis* [*Toroisporis*] *eocenicus*, *Appendicisporites tricuspidatus*, *Microfoveolatosporis pseudodentatus*) from the Lower Eocene and the Upper Cretaceous. Within the exosporium, two major layers (ectexosporium , endexosporium) can be separated primarily by electron affinity.

An exine ultrastructure of the angiospermous type was found on the Jurassic *Spheripollenites*. The finer structure of the wall in the Upper Cretaceous cf. *Araucariacites* v. *Granulatisporites* fsp. is of an angiospermous character.

The form-genera *Classopollis* and *Classoidites* are well separable by the ultrastructure of the columella layer above the endexine.

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Plate I

Leiotriletes adriennis (R. Pot. et Gell. 1933) W. Kr. 1959 asp. *triplanoid* Kds. 1961

1 — Optical microscopic picture of embedded specimen, examined also ultrastructurally. ×1000.
2 — Ultrastructure of germinal spore wall. ×10 000.
3 — Section from the ultrastructure of the germinal region. ×25 000.
4 — Ultrastructure of extragerminal spore wall. ×25 000.
Ectexosp. = ectexosporium, Endexosp. = endexosporium, L = laesura, x = ectexosporium layer covering laesurae.

Plate II

Toroisporis (*Toroisporis*) *eocenicus* Kds. 1966

1, 2 — Optical microscopic picture of embedded specimen, examined also ultrastructurally. ×1000.
3 — Ultrastructure of extragerminal spore wall. ×50 000.
4 — Ultrastructure of torus. ×25 000.
Ectexosp. A = external layer of ectexosporium; Ectexosp. B = internal layer of ectexosporium; Endexosp. = endexosporium.

Plate III

Appendicisporites tricuspidatus Weyl. and Greif. 1953

1 — Optical microscopic picture of embedded specimen examined also ultrastructurally. ×1000.
2, 3 — Ultrastructure of extragerminal spore wall. ×5000.
Ectexosp. = ectexosporium; Endexosp. = endexosporium; M = muri, S = striae.

Plate IV

Microfovealatosporis pseudodentatus W. Kr. 1959

1, 2 — Optical microscopic picture of embedded specimen, examined also ultrastructurally. ×1000.
3 — Ultrastructure of extragerminal spore wall. ×25 000.
4 — Ultrastructure of germinal region. ×25 000.
Mf = microfoveolum; L = laesura; x = wall section covering laesure.

Plate V

Cf. *Araucariacites* v. *Granulatisporites* fsp.

1 — Optical microscopic picture of embedded specimen, examined also ultrastructurally. ×1000.
2 — Tangentional section of columellar layer. ×25 000.
3, 4 — Cross-section of ultrastructure in the wall of the sporomorph. ×25 000.
O = superficial ornamental element; T = tectum, C = columellar layer.

Plate VI

Spheripollenites scabratus Couper 1958

1, 2 — Optical microscopic picture of embedded specimens, examined also ultramicroscopically. ×1000.
3 — Exine ultrastructure of two contacting pollen grains. ×50 000.
4 — Tangentional section of columellar layer. ×50 000.
5 — Survey of the exines examined. ×5000.
6 — Ultrastructure of exine. ×50 000.
T = tectum, C = columellar layer, F = foot layer.

Plate VII

Classoidites glandis Amerom, 1965

1 — Optical microscopic picture of embedded tetrad examined also ultramicroscopically. ×1000.
2 — Section of ultrastructure of exine. ×25 000.
3 — Tangential section from the fourth layer. ×25 000.
4 — Survey from the ultrastructure of the equatorial region. M: 25 000×.
sp = spinae, ch = channels; *1* outernmost layer of the ectexine, "tectum"; *2* thin "columella" layer, *3* "foot layer"; *4* layer similar to the columellar layer of angiospermous pollen grains; *5* endexine.

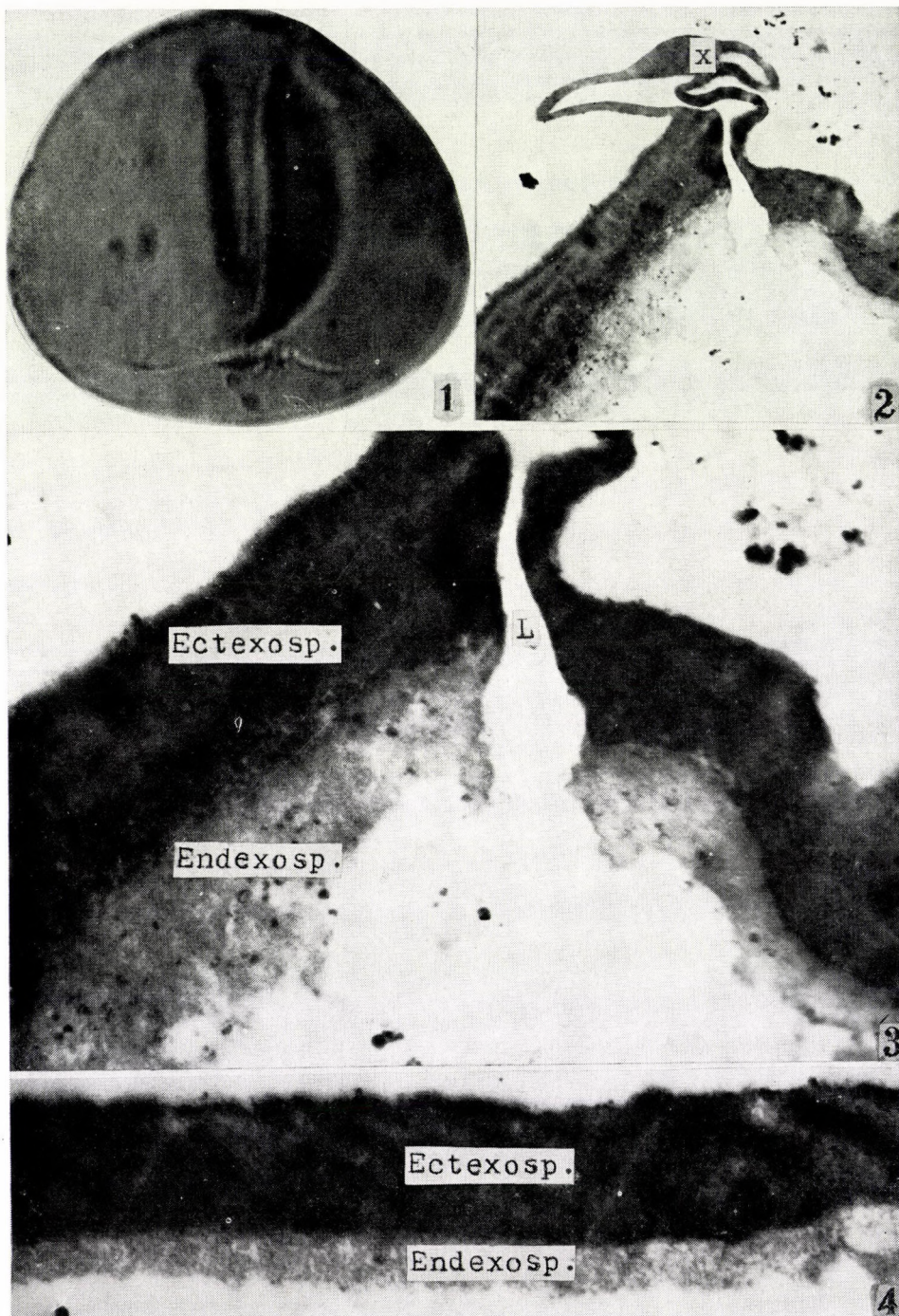



Plate I

Plate II

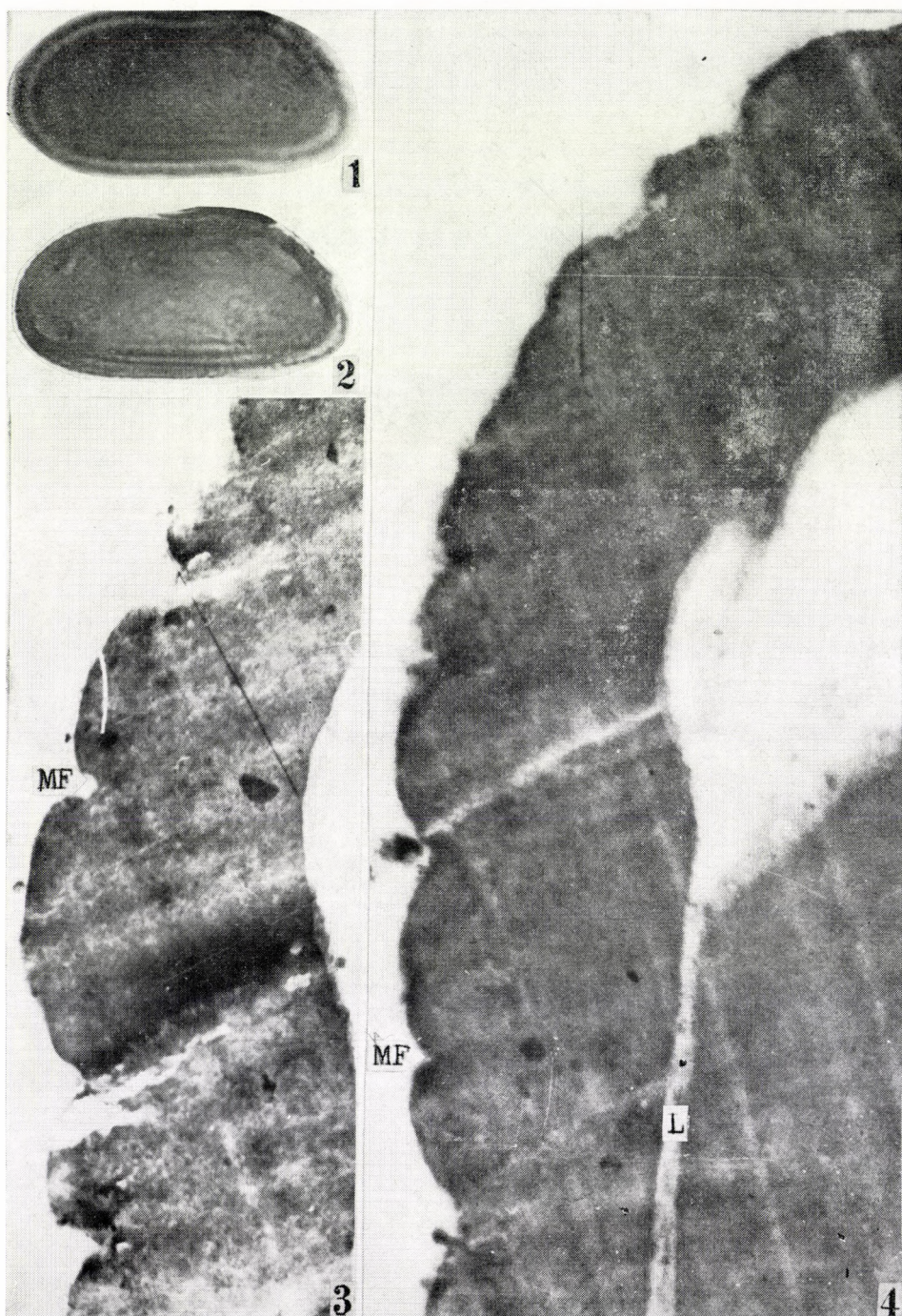



Plate III

Plate IV

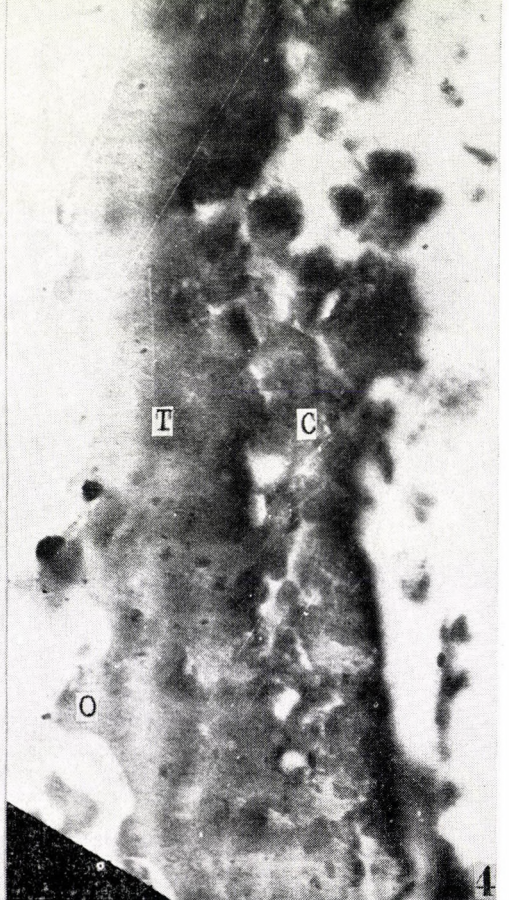
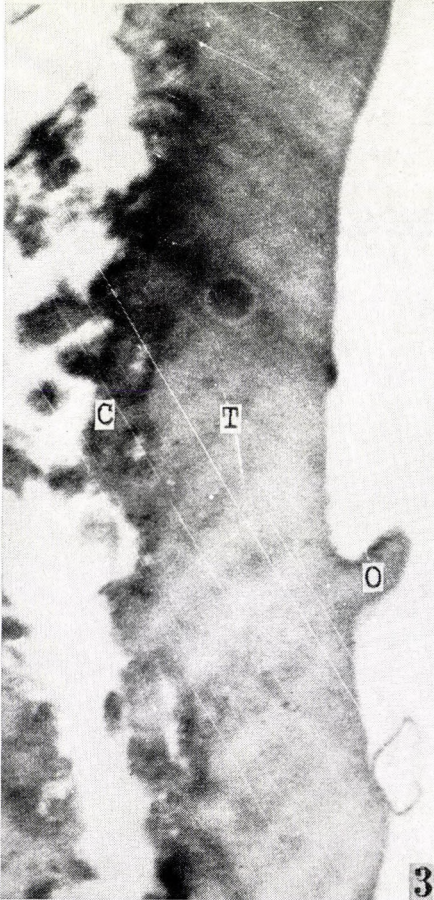
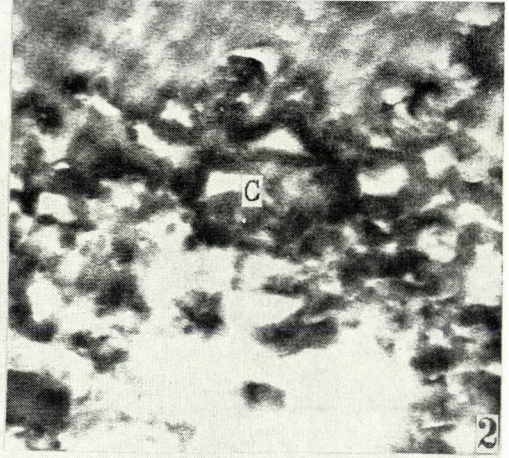
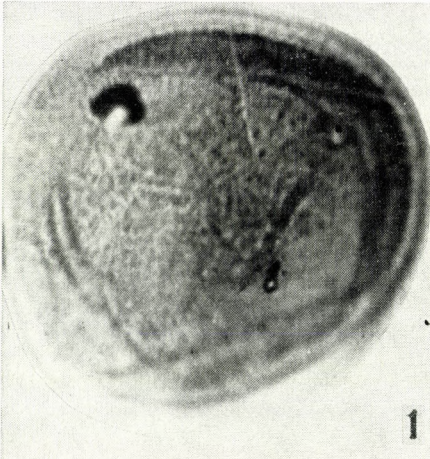
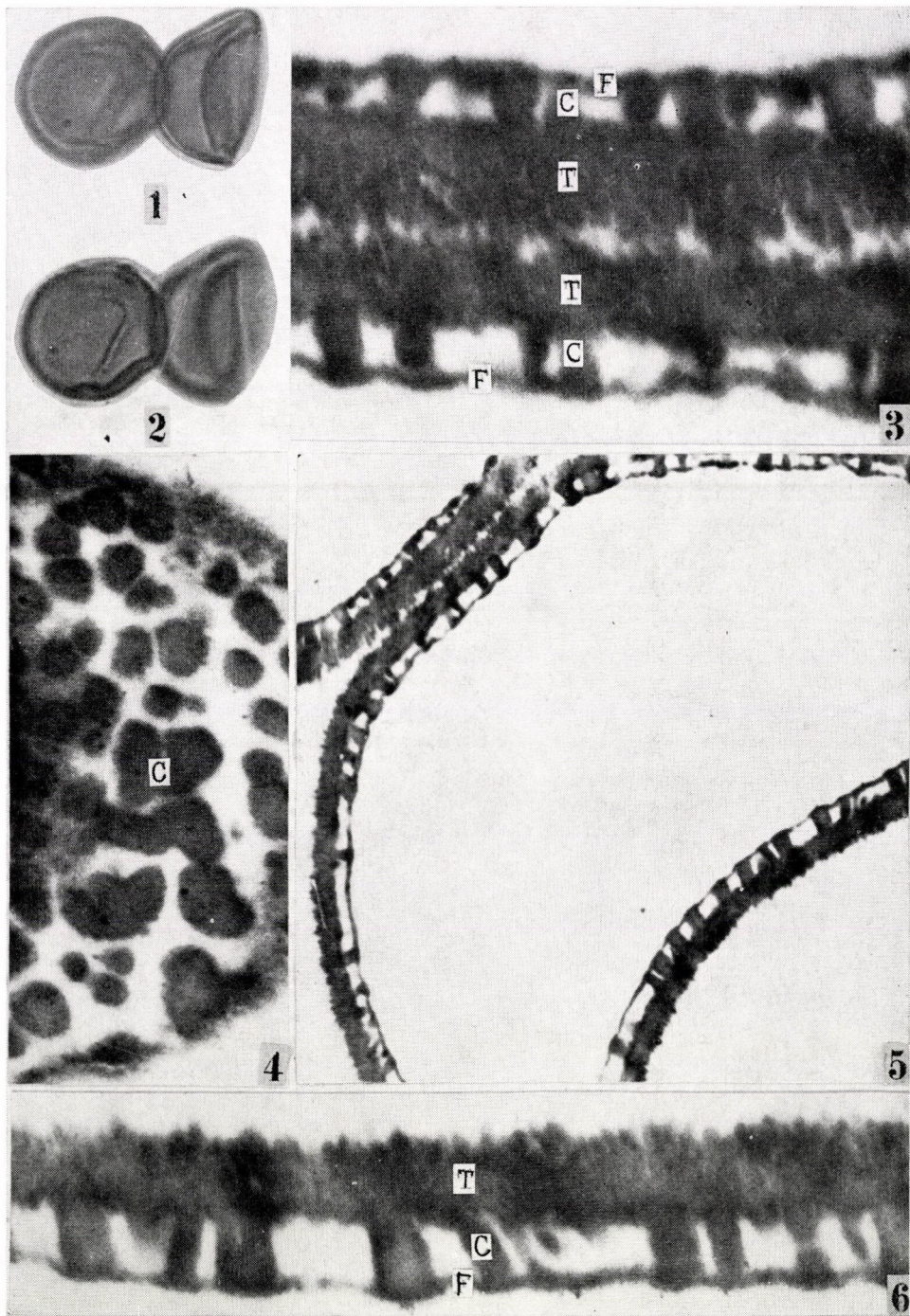
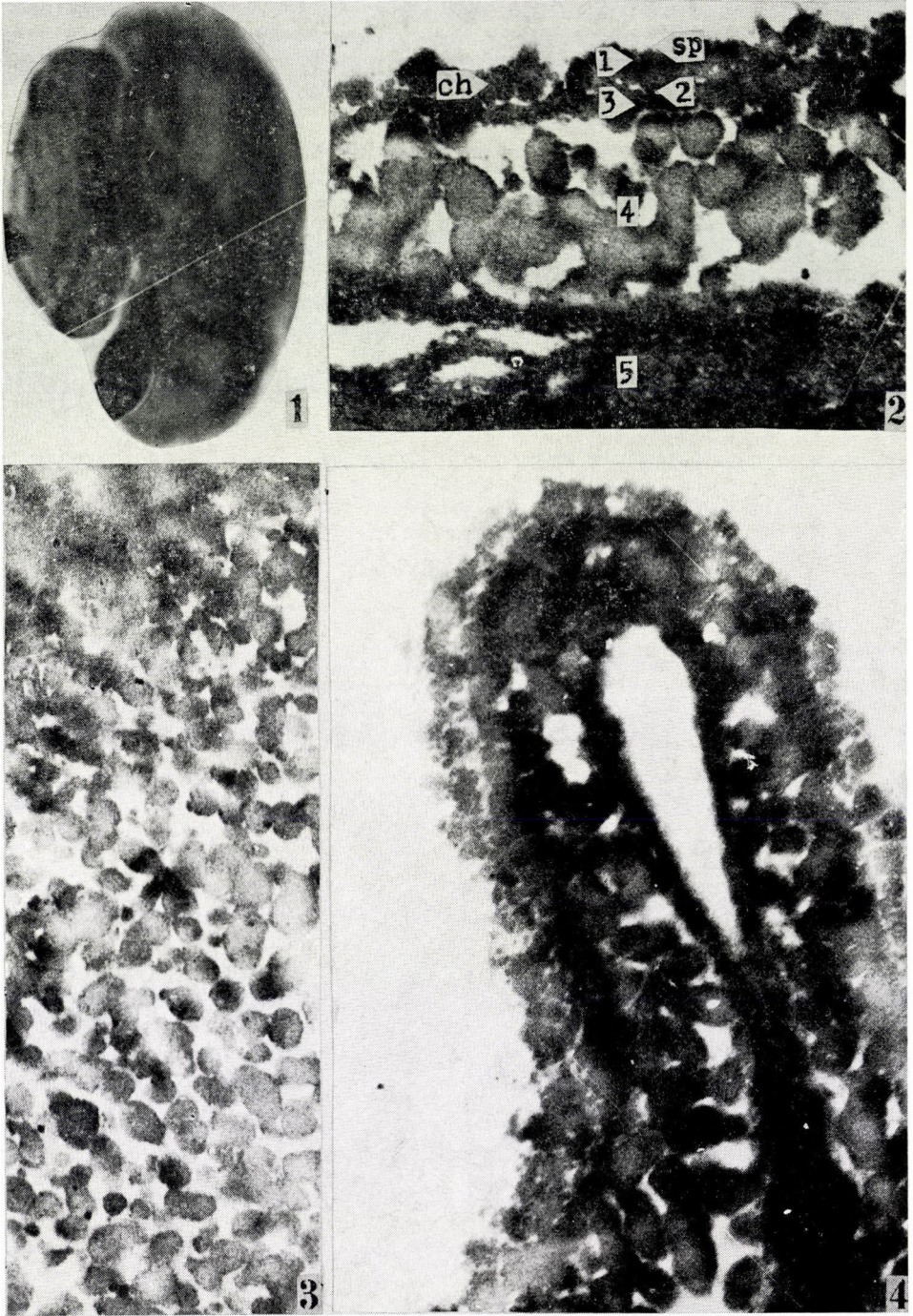



Plate V

Plate VI

Plate VII

Acta Botanica Academiae Scientiarum Hungaricae, Tomus 18 (3—4), pp. 315—322 (1973)

INDOLEACETIC ACID OXIDASE REGULATION IN GENETICALLY TUMOROUS AND NORMAL TOBACCO PLANTS AND IN THEIR TISSUE CULTURES

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The function of the indoleacetic acid oxidase-polyphenol regulation system was studied in *Nicotiana alata*, *N. glauca*, *N. langsdorffii* and in *N. alata* × *N. langsdorffii* F_1 hybrids and in *N. glauca* × *N. langsdorffii* F_1 tumor-forming hybrids and in their tissue cultures of normal and tumorous genotypes. Indoleacetic acid oxidase activity is higher in stems than in leaves. Inversely, the chlorogenic acid content is lower in stems than in leaves. The genetic tumors have a high indoleacetic acid oxidase activity and a low chlorogenic acid content. The tissue cultures studied have a high indoleacetic acid oxidase activity and a low chlorogenic acid content. In tobacco species, hybrids and in the tissue cultures of normal and tumorous genotypes the physiological regulation examined is regular; however, the genetic regulation has a more important role in the formation of genetic tumors. There is a different dominance interaction between the genomes. The data also provide evidence for the homology of stem and genetic tumors.

Introduction

In the previous experiments it has been established that changes in genetic regulation have an important role in the formation of tobacco genetic tumors (KOVÁCS, 1967, 1968, 1970, 1971b, c). Although the role of plant hormone regulation in tumor-formation of *Nicotiana* hybrids was studied by a number of researchers (KEHR and SMITH 1954, BAYER 1965, 1967, BAYER and AHUJA, 1968), the function of physiological regulation mechanisms is less known in the tumor-forming tobacco hybrids.

An important regulator of plant growth and morphogenesis is the indoleacetic acid oxidase-polyphenol system (ZENK and MÜLLER 1963, GARAY et al. 1959, SÁGI and GARAY 1964). The activity of indoleacetic acid oxidase is connected with the polyphenol content of the plant. Different polyphenol derivates of plants are able to regulate the indoleacetic acid oxidase activity. These polyphenols may be cofactors or inhibitors (SCHWERTNER and MORGAN 1966, RABIN and KLEIN, 1957, SACHER, 1961, 1962).

Especially, the role of chlorogenic acid is important in the regulation

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of indoleacetic acid oxidase (IAA-oxidase) function and in growth regulation (RABIN and KLEIN 1957, KOVÁCS et al. 1964—65).

In the present experiments the role of the IAA-oxidase—polyphenol physiological regulating system was studied in tobacco species and hybrids as well as in their tissue cultures.

Material and methods

The experiments were made with *Nicotiana alata* (2n), *N. glauca* (4n), *N. langsdorffii* (2n) and their hybrids as well as with tissue cultures of *N. glauca* and *N. glauca* × *N. langsdorffii* tumor-forming F_1 hybrid (KOVÁCS 1967). The experimental plants were grown in the Biological Station of the L. EÖTVÖS University at Alsógöd. Greenhouse plants of 9—12 leaf phases were used in the experiments. Leaf samples invariably represented leaves from the top as well as from the middle and bottom parts of the plants, so that physiological differences, owing to variations in leaf position, could be eliminated. The same principle prevailed when sampling the stems; whenever it was possible whole stems were tested.

Tissue cultures of 22 months old clones were grown on a modified medium (KOVÁCS 1971a) at 26°C, in dark. Three weeks old tissues were harvested. Both components (organizing and unorganizing) of tumorous tissue cultures were tested (c.f. KOVÁCS 1967).

The activity of IAA-oxidase was measured by a slightly modified method of SEQERIA and LORRANIE (1966). Aceton dry powder of the plant material was extracted with cold sodium phosphate buffer for 3 hours. The centrifuged crude enzyme extract was dialysed against distilled water at 4°C overnight. The enzyme activity was measured on the basis of amount of destroyed IAA. The enzyme activity was expressed as enzyme unit (EU) per mg protein. 1 EU is 1 μg destroyed IAA per minute at 25°C. Reaction mixture: 0.1 M NaH_2PO_4 buffer (pH 4.5), 10^{-4} M $MnCl_2$, 10^{-4} M 2,4-dichlorophenol and 4×10^{-4} M IAA (50 μg/ml), plus dialyzed enzyme extract. The total volume was 2 ml. The reaction mixture was shaken for 10 minutes at 25°C. Reaction was stopped by GORDON and WEBER reagent; IAA content of reaction mixture was measured by GORDON and WEBER reagent (1951). The amount of enzyme used could not maximally destroy more than 20 μg IAA in 10 minutes.

The polyphenols were extracted by 96% etanol (5ml/g plant material) at room temperature for 2 hours. The extract was evaporated and the residue dissolved in a given volume of 70% etanol. Results of this method and that of JOHNSON and SCHAAL (1957) ethanol extraction at 55—65°C in the presence of $K_2S_2O_5$, were similar. The polyphenol extract was spotted on SCHLEICHER and SCHÜLL 2043/b chromatographic paper. The chromatograms were developed in a solvent of butanol, acetic acid, and water, in the proportion 4 : 1 : 2 (v/v) (SARGENT and SKOOG 1960).

Polyphenols were detected by FOLIN—CIOCALTEU-reagent 0.1% $FeCl_3$, nitrite-reagent, NH_3 treatment, and by ultraviolet fluorescence (BLOCK, DURRUM, ZWEIG 1958, HAIS and MACEK 1963).

The chlorogenic acid spot was extracted by distilled water from the paper and the amount of chlorogenic acid was measured by ultraviolet absorption at 313 nm (on the basis of a chlorogenic acid standard curve). Measuring at 313 nm was as suitable as that at 326 nm. The determination of dry matter was made by a method described by KOVÁCS (1971c). Protein was measured by the method of LOWRY et al. (1951).

Results

The extracted IAA-oxidase is characterized by well known (see literature) peculiarities: undialysed enzyme extract cannot destroy IAA within 2 hours; dialysed extract can only destroy IAA in presence of Mn^{++} ions and 2,4-dichlorophenol; the optimum pH of IAA decomposition is 4.5, IAA decomposition can be inhibited by chlorogenic acid at 10^{-6}—10^{-7} M; the

inhibitory effect of low chlorogenic acid concentration disappears after a given lag-period (Fig. 1).

The IAA-oxidase activity of tobacco species and their hybrids is demonstrated in Table 1. The data clearly show that the IAA-oxidase activity is generally higher in stems of the plants than in their leaves. The IAA-oxidase activity in leaves of non-tumor-forming *N. alata*, *N. alata* × *N. langsdorffii* and
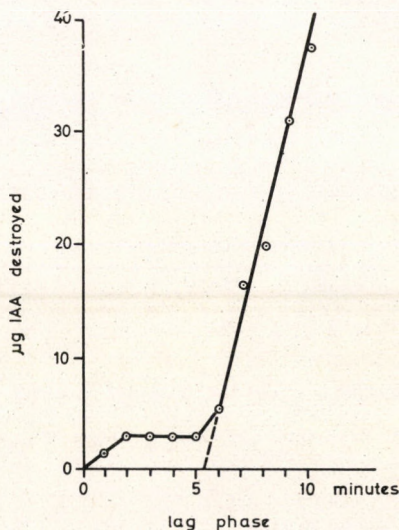
Fig. 1. Inhibitory effect of 10^{-6} M chlorogenic acid on IAA decomposition by IAA-oxidase enzyme

tumor-forming *N. glauca* × *N. langsdorffii* F_1, hybrid is similar. There is no specific difference between tumor-forming and non-tumor-forming plants in IAA-oxidase activity. IAA-oxidase activity of *N. langsdorffii* leaves is higher than that of leaves of other plants. Leaves of *N. glauca* have a lower enzym activity than those of the remaining species and hybrids studied.

Among the stems the lowest IAA-oxidase activity was measured in *N. glauca* and in *N. alata* × *N. langsdorffii* F_1 hybrid. Stems of the remaining plants have a very high IAA-oxidase activity (Table 1). The highest enzyme activity was found in shoots of the tumor-forming hybrids.

IAA-oxidase activity of genetic tumors of *N. glauca* × *N. langsdorffii* F_1 hybrids is high but it is lower than that of the stems (Table 1).

Genetic interactions among the different genomes were also studied concerning IAA-oxidase. An additive or multiplicative action of the genes could not be established. Arithmetic and geometric means of parental values are very close, similar. The genome of *N. langsdorffii* has a dominant effect over that of *N. glauca*. on the other hand, the *N. alata* genome dominates over that

Table 1

IAA-oxidase activity and chlorogenic acid content of tobacco species and their hybrids

Plants	Organs	IAAO* activity	CHLA** content	
		EU / mg protein	mg / g dry weight	IAAO / CHLA
N. glauca	leaf	26.6 ± 9.7	3.08 ± 0.29	8.6
	shoot	298.8 ± 58.6	0.74 ± 0.07	405.0
N. glauca × *N. langsdorffii*	leaf	37.8 ± 8.2	9.89 ± 0.76	3.8
	shoot	819.2 ± 186.4	3.91 ± 0.67	209.4
	tumor	268.1 ± 16.6	4.33 ± 1.19	61.9
N. langsdorffii	leaf	64.4 ± 10.2	20.18 ± 4.55	3.2
	shoot	602.8 ± 50.4	3.42 ± 0.23	176.3
N. alata × *N. langsdorffii*	leaf	42.9 ± 4.7	26.90 ± 2.33	1.6
	shoot	322.8 ± 5.0	2.78 ± 0.29	116.0
N. alata	leaf	40.6 ± 9.6	13.34 ± 1.90	3.0
	shoot	466.3 ± 65.0	3.16 ± 0.28	147.5

* IAAO IAA oxidase
** CHLA chlorogenic acid

of *N. langsdorffii*. (Dominance: $G < L$, $L \leqq A$.) A positive overdominance effect was established in the tumor-forming hybrid stem while a negative one could be experienced in the non-tumor-forming (*langsdorffii-alata*) hybrid stem (see Table 1).

The chlorogenic acid content of the plants was higher in leaves than in stems (Table 1). Among the leaves the lowest level of chlorogenic acid content occurred in *N. glauca*. The highest chlorogenic acid content was measured in leaves of *N. alata* × *N. langsdorffii* F_1 hybrids and in *N. langsdorffii*. The tumor-forming *N. glauca* × *N. langsdorffii* F_1 hybrid leaves have an average and not an unusual level of chlorogenic acid (Table 1) content.

Stems of *N. glauca* have a minimum of chlorogenic acid content. In the stems of the remaining plants the chlorogenic acid content is similar. There are no important differences among the values of chlorogenic acid level (Table 1).

The chlorogenic acid content of genetic tumors is low but it is higher than that of stems (Table 1).

Table 2

IAA oxidase activity, chlorogenic acid content and growth of tissue cultures of normal and genetically tumorous conditions

Tissue culture		IAAO* activity	CHLA** content		Growth*** rate
Origin	Type	EU / mg protein	mg CHLA / g dry weight	IAAO / CHLA	mg fresh weight / 3 weeks
N. glauca × *N. langsdorffii*	shoot	104.5 ± 9.3	6.22 ± 0.56	16.8	3075 ± 175
	callus	339.3 ± 36.4	9.35 ± 0.60	35.6	682 ± 42
	mean	221.9	7.78	28.5	1878
N. glauca	callus	227.8 ± 13.4	6.50 ± 0.21	39.9	2662 ± 18

* IAAO IAA oxidase
** CHLA chlorogenic acid
*** Kovács 1967

In the case of chlorogenic acid content, the *N. langsdorffii* genome also has a dominant effect over that of *N. glauca*, but it has a weaker effect on the *N. alata* genome (Dominance: G < L, L < A). The arithmetic and geometric means of parental values are also similar to each other.

In the tissue cultures of a genetically tumorous condition, derived from *N. glauca* × *N. langsdorffii* F_1 hybrids, there is more than a threefold difference between the IAA-oxidase activity of the shoot parts and the unorganized callus parts. The shoot parts have a low IAA-oxidase activity while the unorganized callus has a high enzyme activity (Table 2).

The IAA-oxidase activity of the normal *N. glauca* callus is higher than that of the shoot part of the tumorous tissue cultures, but the enzyme activity of the normal callus is lower than that of the callus part of a tissue in a genetically tumorous condition (Table 2).

The chlorogenic acid content of shoot parts of the tumorous cultures is lower than that of their unorganized callus parts. In the normal callus tissues of *N. glauca* the chlorogenic acid content is similar to the chlorogenic acid content of the shoot parts of the tumorous cultures (Table 2).

It appeared generally that a high IAA-oxidase activity of tissues is accompanied by a low chlorogenic acid content and, inversely, in the presence of a high chlorogenic acid level a low enzyme activity could be measured (Tables 1 and 2).

The ratio of IAA-oxidase activity per chlorogenic acid content is very high in stems and low in leaves (Table 1). This ratio of the genetic tumors is between the values of stems and leaves and similar to the IAA-oxidase per chlorogenic acid ratio of tissue cultures.

Discussion

The present experiments clearly show a close correlation between the IAA-oxidase activity and the chlorogenic acid content of plant tissues. A high level of chlorogenic acid content of tissues inhibits their IAA-oxidase activity (e.g. in leaves of the plants; see Table 1). A low chlorogenic acid content is accompanied by high IAA-oxidase activity (e.g. in shoots of the plants; see Table 1). Thus, our experiments provide evidence for a regular function of the IAA-oxidase-polyphenol system, well known in the literature (RABIN and KLEIN 1957, SCHWERTNER and MORGAN 1966), in the tobacco species and hybrids examined.

Our data are in accordance with MEUDT's experiments (1970). He found a low IAA-oxidase activity in leaves of *N. glauca* and a higher enzyme activity in leaves of *N. langsdorffii* as well as in genetic tumors of their hybrids. MEUDT could detect the highest IAA-oxidase activity in leaves of the tumor-forming hybrids. This cannot be confirmed by our data. According to MEUDT, the products of oxidative IAA transformation by IAA-oxidase would be important in the genetic tumor formation.

The IAA-oxidase activity of the genetic tumors is high and their chlorogenic acid content is low. These values are similar to stem values. It means that this physiological regulation system functions normally in the tumors too. Though the genetic tumors have a high IAA-oxidase activity, nevertheless there is a high auxin content in the tumors (KEHR and SMITH 1954, BAYER and HAGEN 1964, BAYER 1965, 1967). This fact can be explained by the increased auxin synthesis in tumors (increased tryptophane conversion to IAA; HENDERSON and BONNER 1952), and rather by the increased biosynthetic activity of genetic tumors due to derepression of genetic activity (KOVÁCS 1967, 1971b, c, d). The high degree of derepression may result also in an increased synthesis of IAA-oxidase and IAA synthezizing enzymes.

Data of the present experiments provide evidence for a primary role of genetic regulation system in the formation of genetic tumors. These agree with the earlier experiences (KOVÁCS 1967, 1970, 1971b, c, d).

In the tissue cultures, the physiological regulation of IAA-oxidase-polyphenol system is also normal. Results of the present experiments are in accordance with KOVÁCS's earlier experiences (1967): a high IAA-oxidase activity is accompanied by a low growth rata of tissue cultures and, inversely, a low IAA-oxidase activity is accompanied by a high growth rate (see Table 2; KOVÁCS 1967).

According to literature, tumorous tissue cultures have a high auxin content. Nevertheless, they also have a high level of IAA-oxidase (Table 2). The growth of the tissue cultures of a tumorous genotype cannot be influenced by IAA significantly in the interval of 10^{-4} M to 10^{-7} M concentrations

(Kovács 1969). That is, the data presented also confirm the primary role of genetic regulation factors in behaviour of the tissue cultures of a tumorous genotype (c.f. Kovács, 1967; 1969; 1970; 1971d).

The dominant effect of the *N. langsdorffii* genome has been detected by Kovács's experiments (1971c). Our present experiments support the dominant effect of the *langsdorffii* genome.

The homology of stem and genetic tumor as well as of genetic tumor and organizing tissue culture of a genetically tumorous condition has also been described by Kovács (1968, 1971b, c). This homology is proved also by our present data. First, the level of IAA-oxidase and chlorogenic acid and their ratio are similar in both stems and tumors; on the other hand, the level of IAA-oxidase activity, chlorogenic acid and their ratio are the same in the genetic tumors and in the tumorous tissue cultures (c.f. Tables 1 and 2).

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UNTERSUCHUNG ÜBER DIE ZONATIONS- UND PRODUKTIONSVERHÄLTNISSE IM ÜBERSCHWEMMUNGSGEBIET DER DRAU I. VERLANDUNG DER TOTEN ARME UND DIE ZONATIONEN DES BODENS UND DER VEGETATION IM INUNDATIONSGEBIET DER DRAU

Von

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The paper examines the alluvial process in the inundation basin of the river Drava, and the various zones of soil and flora. In the alluvia and in their zones, three soil types (inundation meadow soil, marshy meadow soil and moorland) come into existence, according to water and moisture conditions. The zonal arrangement of vegetation occurs in accordance with the soil and water conditions. Concerning the outer zone of the alluvia, the organogenous succession series, closing with swamp wood. is characteristic. The soils of the various vegetation zones are significantly different in several physical and chemical factors. The inferences of the paper primarily relevant to the areas alluviated from the deposit of the river Drava.

Einleitung

Der Verlandungsprozess von stehenden Gewässern, toten Flussarmen u. dgl., die Entstehung der verschiedenen litoralen Zonationen gehört seit langher zu den Untersuchungsthemen der Pflanzengeographie (vgl. ELLENBERG, 1963, mit ausführlicher Darstellung der einschlägigen Literatur). Die Zonationsglieder hatte man häufig als Elemente einer Sukzessionsfolge angesehen, und dementsprechend wurde das räumliche Nebeneinander als zeitliches Nacheinander aufgefasst. Das Interesse für die Zonationsverhältnisse der Vegetation hatte die Nebenfolge, dass die Untersuchungen über die Bodenverhältnisse ins Hintertreffen kamen. Die meisten Beiträge zu dieser Thematik befassten sich mit den Beziehungen zwischen dem Wasser und der Pflanzenwelt, wobei der Einfluss der hydrologischen Verhältnisse (Wasserbedecktheit, Tiefe des Grundwassers, Feuchtigkeitsgehalt des Bodens) auf die Bodenverhältnisse sowie die Entstehung und Bildungsprozesse der verschiedenen Bodenfaktoren ausser acht gelassen wurde.

Auf dem insgesamt 306 ha grossen Area der 32 Altarmteiche und 27 toten Arme im Überschwemmungsgebiet der Drau (vgl. Magyarország Hidrológiai Atlasza IV/1. Magyarország állóvizeinek katasztere, VITUKI, Budapest

1962, 1—70) konnten die Zonationsverhältnisse und die Verlandungsprozesse gut untersucht werden (Abb. 1). Für die toten Arme und die Altarmteiche erwies sich der nährstoffreiche, chemisch fast neutrale oder alkalische eutrophe, $Ca(HCO_3)_2$-haltige Wassertyp als kennzeichnend (Abb. 2).

Im Zuge der Untersuchungen, die wir im Auftrage der »Wasserwirtschaftsdirektion Süd-Transdanubien« im Überschwemmungsgebiet der Drau mehrere Jahre hindurch angestellt haben, konnte festgestellt werden, dass sich die
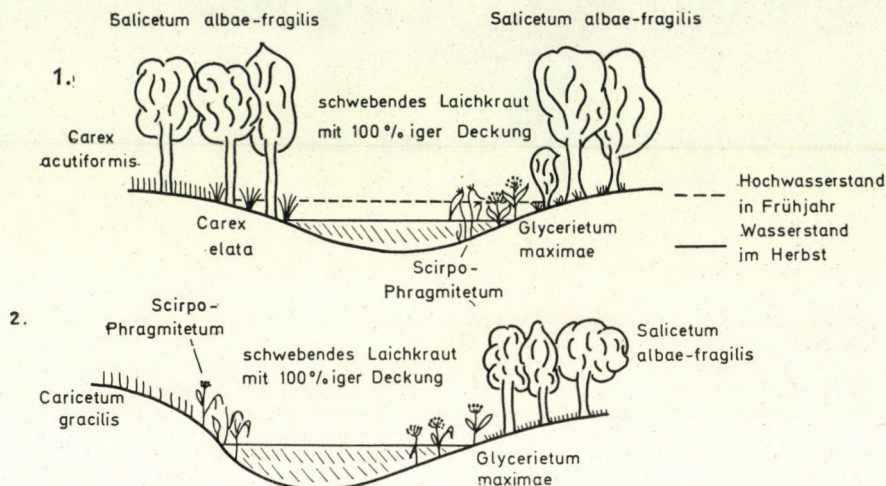
Abb. 1. Zonationsverhältnisse im östlichen Lauf des toten Armes von »Cun-Majlátpuszta«

— im Sinne der Stromrichtung der Drau — oberen, westlichen Teile der Altarme in einem älteren Stadium der Verlandung befinden, und dass bei ihnen die Vegetationsentwicklung — je nach den Bodenverhältnissen — bereits das Stadium der Moor- bzw. Auwälder erreicht hat. In den höheren Lagen treten auch Hainbuchen-Eichen-Wälder auf. Übergangsbestände von Auwald und *Querco-Carpinetum* sind dabei nicht selten. Die meisten, östlichen Altarmläufe befinden sich in einem jüngeren Stadium des Verlandungsprozesses. Hier gibt es noch häufig offen Wasserflächen, m. a. W. stehende Altarmteiche, mit verschiedenen Schilf- und Laichkrautgesellschaften (Abb. 3 u. 4).

Zu ähnlicher Einsicht ist auch CHOLNOKY (1907) bei der Untersuchung der Theiss-Altarme gelangt. Nach seiner Erkenntnis beginnt der Verlandungsprozess in der Weise, dass der Fluss allmählich die obere und die untere Mündung der durchschnittenen Schleife auffüllt — mit Ablagerungen wie bei den Sandbänken am Ufer. Die untere Mündung kommt viel später zum Verschluss als die obere — oft bleibt sie noch sehr lange offen, und schliesst sich erst dann in einem rascheren Tempo, wenn der tote Arm von oben her schon kaum etwas Wasser erhält.
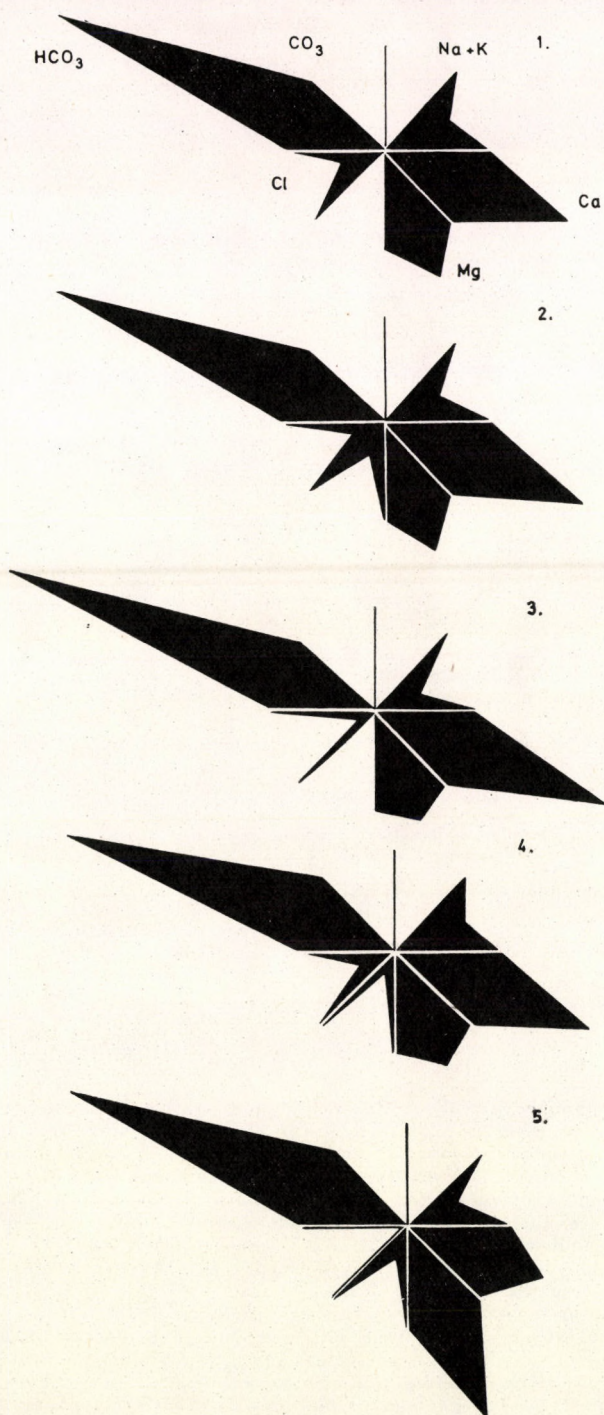
Abb. 2. Hydrochemische Diagramme der Altarmteiche im Überschwemmungsgebiet der Drau. 1: Barcs–Darány, 2: Alsórigóc, 3: Révfalu, 4: Zaláta, 5: Drávasztára
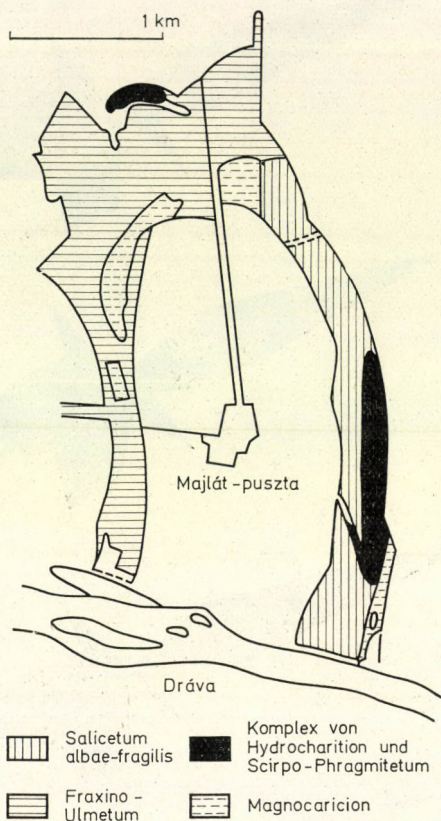
Abb. 3. Kartenskizze der wichtigeren Pflanzengesellschaften des toten Armes von »Cun-Szaporca«

Ziel der Untersuchungen, Mustergebiet

Die Untersuchungen verfolgten das Ziel, die in verschiedenen Stadien der Verlandung stehenden Altarmabschnitte zu erforschen, die hydrologisch bedingten Boden- und Vegetationszonationen des Altarmufers sowie die ökologische Reihenfolge der verschiedenen Pflanzengesellschaften zu bestimmen. Des weiteren gesellte sich als Zielsetzung dazu: die Bestimmung der Bodendifferenzen zwischen den Pflanzengesellschaften der einzelnen Zonationen wie auch Ermittlung dessen, was für zönologische und pedologische Verhältnisse die sich in unterschiedlichen Verlandungsstadien befindlichen Altarme kennzeichnen.

Für die eingehenderen Untersuchungen wurden zwei Abschnitte des sich in der Nähe der Gemeinde »Lakócsa« befindlichen Altarmsystems auserwählt (Abb. 5), und zwar solche, bei welchen der Verlandungsprozess verschiedene Stadien erreicht hat.

Im Falle des östlichen Altarmteils ist — wie bei den meisten Altarmen des Drau-Binnenlandes überhaupt — ein tief eingeschnittener Uferabschnitt charakteristisch; die einzelnen Pflanzengesellschaften bedecken nur schmale Streifen. Für den östlichen Arm ist ausserdem noch ein mit *Scirpo-Phragmitetum typhetosum* bedeckter Altarmteich kennzeichnend (Abb. 6). Der ältere, bereits verlandete und mit einer Gross-Seggenwiese (bzw. mit Moorwald) verriegelte Altarmlauf zeichnet sich durch sanft abfallenden Uferstrich aus, mit breiten und verhältnismässig ausgedehnten Zonen (Abb. 7).
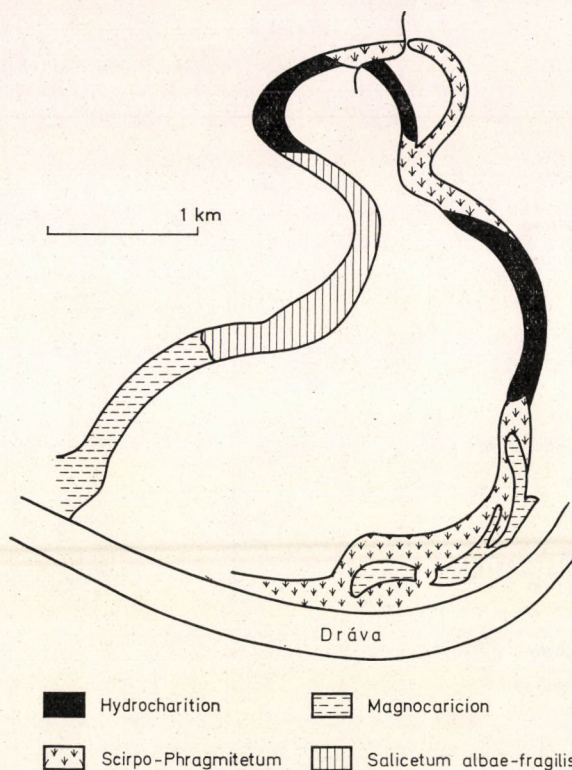
Abb. 4. Kartenskizze der wichtigeren Pflanzengesellschaften des toten Armes von »Szaporca»
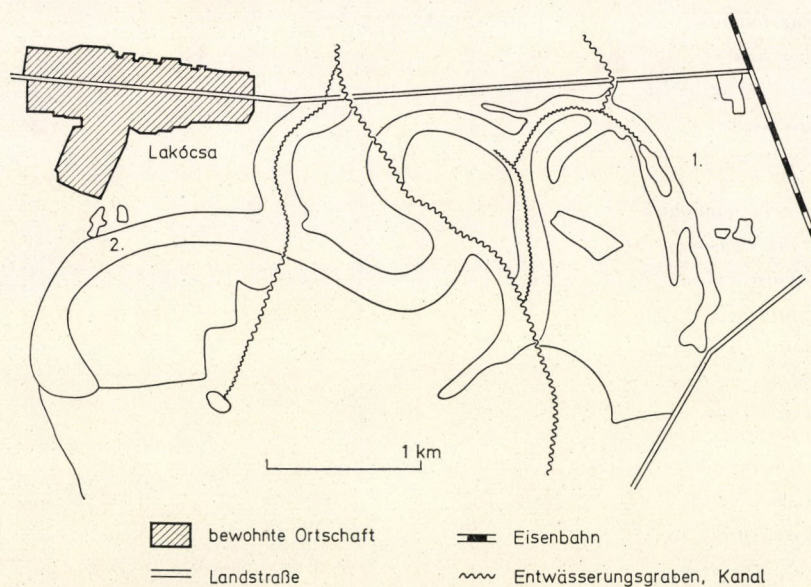
Abb. 5. Kartenskizze des toten Armes von »Lakócsa«

Tafel 1

Ökologische Reihe von Pflanzengesellschaften im östlichen Lauf des toten Armes von Lakócsa (1)

Pflanzengesellschaften	1	2	3	4	5
W x̄ (Bodenfeuchtigkeitsindikation)	4,92	5,58	7,58	9,00	10,30
3 *Achillea millefolium*	.	1	.	.	.
3 *Euphorbia cyparissias*	.	+	.	.	.
3 *Galium mollugo* s. l.	.	1	.	.	.
3 *G. verum*	1	1—2	.	.	.
3 *Linaria vulgaris*	+	.	.	.	.
3 *Myosotis arvensis*	+—1	.	.	.	.
4 *Anthoxanthum odoratum*	+—1	.	.	.	.
4 *Cirsium arvense*	+	.	.	.	.
4 *Galium cruciata*	+	.	.	.	.
4 *Lotus corniculatus*	+	.	.	.	.
4 *Melandryum album*	+	.	.	.	.
4 *Ononis arvensis*	+	+—1	.	.	.
4 *Plantago lanceolata*	1	+	+	.	.
4 *Veronica chamaedrys*	+—1	+—1	.	.	.
4 *Vicia cracca*	+—1	+	+	.	.
5 *Arrhenatherum elatius*	2—3	.	.	.	.
5 *Daucus carota*	+	+	.	.	.
5 *Holcus lanatus*	1—2	.	.	.	.
5 *Rumex acetosa*	.	.	1	.	.
5 *Taraxacum officinale*	.	+—1	.	.	.
5 *Urtica dioica*	.	.	.	+	.
6 *Bromus commutatus*	1	.	.	.	.
6 *Centaurea pannonica*	+—1	+	.	.	.
6 *Dactylis glomerata*	2	+	.	.	.
6 *Pastinaca sativa*	1	+	.	.	.
6 *Poa pratensis*	2	1	+	.	.
6 *Potentilla reptans*	.	.	+	.	.
6 *Trifolium pratense*	+—1	+—1	.	.	.
6 *Trisetum flavescens*	1	.	.	.	.
7 *Cirsium canum*	.	+	.	.	.
7 *Festuca pratensis*	.	3—4	.	.	.
7 *Lathyrus pratensis*	.	+—1	.	.	.
7 *Ranunculus acer*	.	1—2	1	.	.
7 *Succisella inflexa*	.	.	1	.	.

Tafel 1 (cont.)

Pflanzengesellschaften	1	2	3	4	5
W x̄ (Bodenfeuchtigkeitsindikation)	4,92	5,58	7,58	9,00	10,30
8 *Alopecurus pratensis*	1	+−1	1−2	.	.
8 *Festuca arundinacea*	2	.	.	.	.
8 *Lychnis flos-cuculi*	+−	+	1	.	.
8 *Myosotis palustris*	.	.	+	.	.
8 *Ranunculus repens*	.	+	1−2	.	.
8 *Symphytum officinale*	.	.	2	1−2	1
9 *Calystegia sepium*	.	.	1−2	1−2	.
9 *Carex vulpina*	.	.	3	+−1	.
9 *Lycopus europaeus*	.	.	+	+	.
9 *Mentha aquatica*	.	.	1	1	+
10 *Carex acutiformis*	.	.	.	1−2	.
10 *C. elata*	.	.	.	3−4	.
10 *Galium palustre*	.	.	+−1	.	.
10 *Iris pseudacorus*	.	.	1	1	.
10 *Phragmites communis*	.	.	.	.	1
10 *Rorippa amphibia*	.	.	.	1	1−
10 *Typha latifolia*	.	.	.	1	3−4
10 *Urtica kioviensis*	.	.	.	.	2
11 *Hydrocharis morsus-ranae*	.	.	.	.	1−2
11 *Lemna minor*	.	.	.	.	2
11 *Oenanthe aquatica*	.	.	.	.	+
11 *Spirodela polyrrhiza*	.	.	.	.	1−
11 *Utricularia vulgaris*	.	.	.	.	2

Die Vegetationsverhältnisse der Altarmläufe

A. Auf dem Mustergebiet des Ostlaufes des toten Arms von Lakócsa (Stichprobenentnahmestelle 1) lassen sich — den hydrologischen (Bodenfeuchtigkeits-) und pedologischen (Bodenbeschaffenheits-) Verhältnissen entsprechend — fünf Pflanzengesellschaften unterscheiden (Tafel 1, vgl. Abb. 6).

Die auf Grund der Bodenfeuchtigkeitswerte auf der Tafel angeordneten Pflanzengesellschaften sind

1. *Arrhenatheretum elatioris* s. l.
2. *Festucetum pratensis*
3. *Caricetum vulpinae*

4. *Caricetum elatae*
5. *Scirpo-Phragmitetum typhetosum.*

Bei der tabellarischen Aufführung der Arten wurde von der Bodenfeuchtigkeitsindikation ausgegangen. (Näheres über die W-Indikationswerte s. ZÓLYOMI und PRÉCSÉNYI, 1964, ZÓLYOMI et al. 1967.)
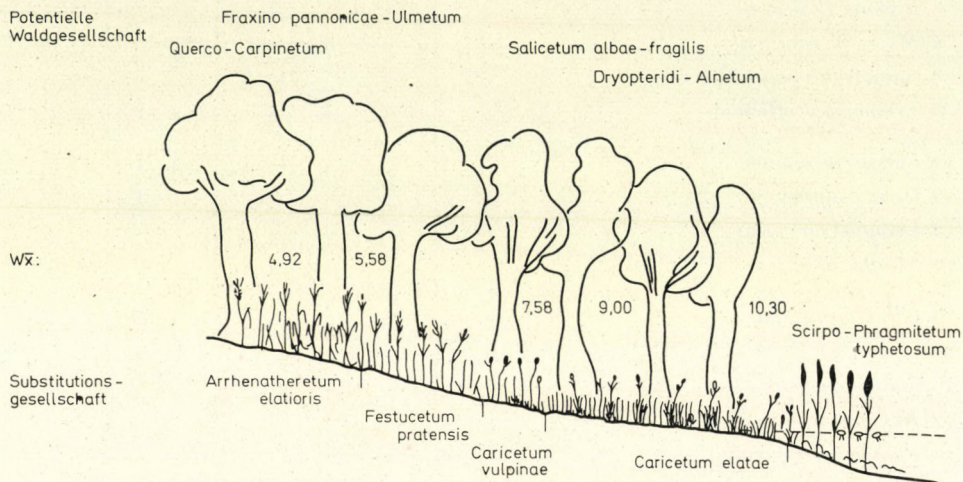
Abb. 6. Die Zonation im östlichen Lauf des toten Armes von »Lakócsa« und die Messdaten der Bodenuntersuchung

Die Zonation des Ostlaufes des toten Armes von Lakócsa
Mustergebiet 1

Mittelwerte der Daten der Bodenuntersuchung n : 5					
pH im Wasser	5,8	6,2	6,2	6,3	6,3
y_1	6,9	5,9	6,9	11,3	9,4
hy	2,4	2,8	3,7	6,0	5,7
Humus %	4,8	7,5	11,5	21,6	16,5
Q	1,176	2,033	1,892	0,838	1,132
N %	0,267	0,380	0,548	0,972	0,640
NH_3-N mg/100 g	0,2	0,2	0,3	0,4	0,4
NO_3-N mg/100 g	0,4	0,5	0,5	6,05	1,0
K_2O mg/100 g	8,6	9,4	9,9	16,1	20,1
P_2O_5 mg/100 g	21,0	6,6	4,1	6,9	8,7
Ca mval/100 g	20,7	30,9	39,1	44,2	36,7
S mval/100 g	26,1	37,2	47,6	54,5	44,8
T mval/100 g	41,9	48,9	64,0	75,7	69,2
V %	62,0	75,8	75,0	71,9	64,8

Das Vorkommen von Arten mit dem Indikationswert W : 5 ist gewöhnlich für die supralitorale Zone typisch, m. a. W. für Stellen, die keinen Überschwemmungen ausgesetzt sind. Die Standorte der Arten mit W : 6 können fallweise (im Frühling) auf kurze Zeit unter Wasser zu stehen kommen. Die Arten mit den Werten W : 7, 8 deuten auf die frühjährlich regelmässig wiederkehrende Überschwemmungen des Standortes. Die Standorte der Arten mit W : 9, 10 sind während des grössten Teiles des Jahres mit Wasser bedeckt (oder reicht das Grundwasser bis knapp an die Oberfläche). Der Artenwert W : 11 gilt für ständige Wasserbedecktheit (d. h. bei Wasserpflanzen).

1. *Arrhenatheretum elatioris* kommt in der höchstgelegenen Uferzone im obersten Horizont (von 100 m Seehöhe, auf einer Terrasse des Alt-Holozän) auf Wiesenboden mit üppig bewachsenen Standorten (W $\bar{x}$: 4,92) vor. Es handelt sich um eine »Ersatzgesellschaft« an Stelle des einstigen Eichen-Hainbuchenwaldes (*Querceto-Carpinetum*). Die Mähwiese als Standort des Glatthafers ist der unmittelbaren Überflutung d. h. dem Frühjahrhochwasser nicht mehr ausgesetzt. Auch die Wassertiefe im Vorfrühling bleibt gewöhnlich unter 50 cm; in den Sommermonaten kann sie sogar unter 1,5—2,0 m sinken. In der floristischen Zusammensetzung der Mähwiese spielen die Kennarten für mässig frische (W : 4), frische (W : 5) und mässig feuchte (W : 6) Standorte die Hauptrolle.

2. *Festucetum pratensis* hat seine Standorte in einer tiefer gelegenen Zone mit höherem Grundwasserniveau (im Frühjahr steht das Wasser bis zur Oberfläche oder nahe dazu) auf frisch-feucht alluvialem Wiesenboden (W $\bar{x}$: 5,58). In der floristischen Zusammensetzung erscheinen vorwiegend die einen frischen (W : 5), einen mässig feuchten (W : 6) und einen feuchten (W : 7) Standort anzeigenden Arten. Auf dem Standort von *Festucetum pratensis* können Auwälder (*Fraxino-Ulmetum*, *Salicetum albae-fragilis*) entstehen.

3. *Caricetum vulpinae* gehört zu den charakteristischen Pflanzengesellschaften im ungarischen und jugoslawischen Teil des Überschwemmungsgebietes der Drau. Er erscheint gewöhnlich schon in den tieferen Lagen der Altarme, oft unmittelbar im Anschluss an die Zone der blütenbildenden Gross-Seggengesellschaften, auf sumpfigem Wiesenboden. Der Grundwasserspiegel liegt den längsten Teil des Jahres hindurch an der Oberfläche oder in nächster Nähe dieser (W $\bar{x}$: 7,58). Für die standortliche Beschränktheit, die verhältnismässig enge ökologische Amplitude der Assoziation zeugt der Umstand, dass an der floristischen Zusammensetzung hauptsächlich die Kennarten von mittelmässig wässrigen (W : 8) und wässrigen (W : 9) (staunassen) Standorten teilhaben.

4. *Caricetum elatae* erscheint auf sumpfigem Wiesenboden und auf Moorboden in der Rolle einer typischen »Verlandungsgesellschaft«, als Bindeglied zur Randzonation des Altarms, welche ein Röhricht bzw. eine Rohrkolbengesellschaft, gelegentlich eine mit Laichkraut bedeckte Wasserfläche trägt.

Tafel 2

Ökologische Reihe von Pflanzengesellschaften im westl. Lauf des toten Armes von Lakócsa (2)

Pflanzengesellschaften	1	2	3	4	5	6
W x̄ (Bodenfeuchtigkeitsindikation)	4,86	5,85	6,86	7,55	8,52	9,00
2 *Festuca pseudovina*	(+)	.	.	.	.	.
3 *Galium mollugo* s. l.	(+)	.	.	.	.	.
3 *G. verum*	(+)	.	.	.	.	.
4 *Achillea millefolium*	1	1—2	+	.	.	.
4 *Anthoxanthum odoratum*	(+)	.	.	.	.	.
4 *Carex spicata*	.	1	1	(+)	.	.
4 *Centaurea jacea* s. l.	(+)	.	.	.	.	.
4 *Crepis biennis*	.	+	.	.	.	.
4 *Lotus corniculatus*	1	.	.	.	.	.
4 *Ononis arvensis*	1	+	.	.	.	.
4 *Plantago lanceolata*	1	+	.	.	.	.
4 *Veronica chamaldrys*	.	1	.	.	.	.
4 *Vicia grandiflora*	+	.	.	.	.	.
5 *Cerastium vulgatum*	1	1	+	.	.	.
5 *Cichorium intybus*	(+)	.	.	.	.	.
5 *Daucus carota*	1	.	.	.	.	.
5 *Holcus lanatus*	(+)	1	2	(+)	1	.
5 *Lolium perenne*	1—2	.	.	.	.	.
5 *Rhinanthus minor*	1	+	.	.	.	.
5 *Rumex acetosa*	.	.	.	(+)	.	.
5 *R. crispus*	.	1	+	1	+	.
5 *Taraxacum officinale*	1	1	.	.	.	.
6 *Ajuga reptans*	.	.	(+)	.	.	.
6 *Bellis perennis*	1	.	(+)	.	.	.
6 *Bromus commutatus*	3	3	1	.	.	.
6 *Colchicum autumnale*	.	+	.	.	.	.
6 *Dactylis glomerata*	2	.	.	.	.	.
6 *Medicago lupulina*	2—3	2	1—2	.	.	.
6 *Poa pratensis*	(1)	1	1	1—2	.	.
6 *Potentilla reptans*	.	.	.	.	1	+
6 *Prunella vulgaris*	.	.	1	+	.	.
6 *Trifolium pratense*	2	2	1—2	1	.	.
6 *T. repens*	1—2	1	2	.	.	.
6 *Trisetum flavescens*	2	.	.	.	.	.
7 *Carex distans*	.	1	1	+	.	.
7 *C. hirta*	.	.	.	+—1	.	.
7 *Cirsium canum*	.	.	2	(+)	.	.
7 *Festuca pratensis*	1	1—2	3	(+)	.	.
7 *Lathyrus pratensis*	.	1—2	.	.	.	.
7 *Ranunculus acer*	1	2	2	1	.	.
8 *Agrostis alba*	.	.	.	.	.	(+)
8 *Alopecurus pratensis*	.	1	.	1	1	1
8 *Gratiola officinalis*	.	.	.	1	.	.
8 *Juncus inflexus*	.	.	(+)	.	.	.
8 *Lychnis flos-cuculi*	.	1—2	1—2	2	1—2	1
8 *Lysimachia nummularia*	.	.	.	.	1—2	1—2
8 *Myosotis palustris*	.	.	.	.	1	1
8 *Orchis palustris*	.	.	.	+	.	.

Tafel 2 (cont.)

Pflanzengesellschaften	1	2	3	4	5	6
W x̄ (Bodenfeuchtigkeitsindikation)	4,86	5,85	6,86	7,55	8,52	9,00
8 *Ranunculus repens*	.	.	1—2	2—3	1	.
8 *Symphytum officinale*	.	+	+	.	+	+
8 *Taraxacum palustre*	.	.	1	1	.	(+)
8 *Trifolium hybridum*	.	.	.	1	1	.
9 *Cardamine pratensis*	.	1	+	1	1	1
9 *Calystegia sepium*	.	.	.	+	.	.
9 *Carex melanostachya*	.	.	.	.	+	1
9 *C. vulpina*	.	.	.	3	1—2	1
9 *Equisetum palustre*	.	.	.	1—2	.	.
9 *Lythrum salicaria*	.	.	.	.	.	1
9 *Mentha aquatica*	.	.	1	1—2	1	1
9 *Oenanthe fistulosa*	.	.	.	.	+	+—1
9 *Poa trivialis*	.	1	1	1	+	+—1
9 *Polygonum persicaria*	.	.	.	.	+	+
10 *Carex acutiformis*	.	.	1—2	1	2	+
10 *C. elata*	.	.	.	.	1	3
10 *C. vesicaria*	.	.	.	2—3	3	1—2
10 *Eleocharis palustris*	.	.	.	.	.	+
10 *Galium palustre*	.	.	.	.	.	1
10 *Glyceria maxima*	.	.	(+)	(+)	.	(1)
10 *Iris pseudacorus*	.	.	2	1	+	1
10 *Rumex hydrolapathum*	.	.	.	.	.	+
10 *Stachys palustris*	.	.	.	.	.	+
11 *Alisma plantago-aquatica*	.	.	.	.	+	+
11 *Sparganium erectum*	.	.	.	.	1	+

Das Grundwasser steht das ganze Jahr hindurch an der Oberfläche, in den Schlenken zwischen den Bülten (W x̄: 9,00). Die enge ökologische Amplitude derselben Assoziation wird aber auch durch die in der floristischen Zusammensetzung dominierenden Arten vom Werte W : 9 und W : 10 angezeigt.

5. *Scirpo-Phragmitetum typhetosum* auf eutrophem Gyttja ist für das Anfangsstadium der Verlandung der Altarmteiche charakteristisch. *Typha latifolia* kommt bis rund 150 cm Wassertiefe vor.

B. Unser Mustergebiet 2 war die westliche (mittlere), in ihrer Entwicklung ältere Verlandungszone des toten Armes von »Lakócsa«, in welcher keine freie Wasserfläche mehr zu finden war.

Im weniger tief eingeschnittenen Teil des toten Armes, auf dem sanfter abfallenden Uferabschnitt lassen sich sechs Pflanzengesellschaften unterscheiden (Tafel 2, vgl. Abb. 7). Potentielle Waldgesellschaft auf der Altholozän-Terrasse oberhalb des einstigen Inundationsgebietes ist *Querco-Carpinetum*, während auf den höheren und tieferen Horizonten des Jungholozän die Waldgesellschaften *Fraxino pannonicae-Ulmetum* und *Salicetum albae-fragilis* vertreten sind. Im Zentralabschnitt des Totarms kam der Verlandungsprozess in

der Form eines Moorwaldes (*Dryopteridi-Alnetum*) zum Abschluss; zumindest lassen die im nächsten Umkreis auffindbaren Waldüberreste sowie die Lassbäume der verlandeten Altarmabschnitte darauf schliessen. Dort, wo sich ehemals Waldgesellschaften befunden hatten, sind heute — je nach den Boden-
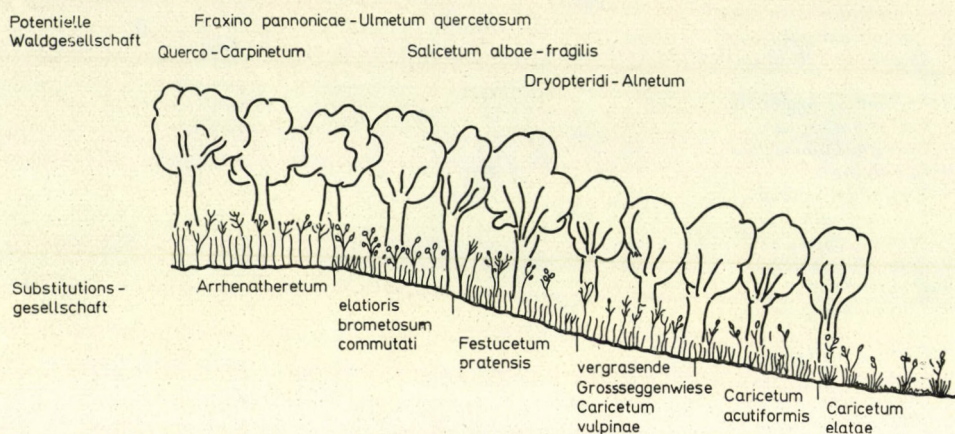
Abb. 7. Die Zonation im westlichen Lauf des toten Armes von »Lakócsa« und die Messdaten der Bodenuntersuchung

Die Zonation des Westlaufes des toten Armes von Lakócsa
Mustergebiet 2

W $\bar{x}$: Mittelwerte der Daten der Bodenuntersuchung n: 10	4,86	5,85	6,86	7,55	8,52	9,00
pH im Wasser	5,9	5,7	6,6	7,3	7,1	7,1
y_1	6,1	8,0	2,2	1,5	3,2	2,8
$CaCO_3$ %	0,0	0,0	0,0	2,2	1,3	1,4
hy	3,0	2,9	4,8	6,7	6,8	8,6
Humus %	5,3	5,9	11,0	16,3	21,4	46,3
Q	1,217	1,445	4,225	3,308	2,495	1,422
N %	0,256	0,324	0,600	0,900	1,112	1,436
NH_3-N mg/100 g	0,4	0,4	0,2	0,3	0,4	0,3
NO_3-N mg/100 g	0,5	0,8	1,6	3,1	6,2	11,4
K_2O mg/100 g	13,7	19,9	17,1	21,2	16,4	11,3
P_2O_5 mg/100 g	18,7	21,8	6,9	1,5	Sp.	Sp.
Ca mval/100 g	23,4	23,0	43,8	67,2	77,0	83,1
S mval/100 g	29,3	28,9	51,4	77,7	85,4	89,3
T mval/100 g	42,9	43,9	64,5	93,4	100,1	110,4
V %	68,4	65,6	80,0	83,2	85,5	89,3

feuchtigkeitsverhältnissen — etwa als Ersatzgesellschaft verschiedene Wiesengesellschaften zu finden.

Die auf Tafel 2 nach den Bodenfeuchtigkeitswerten angeordneten Pflanzengesellschaften sind wie untenstehend:

1—2. *Arrhenatheretum elatioris* s. l.
3. *Festucetum pratensis*
4. *Caricetum vulpinae*
5. *Caricetum acutiformis*
6. *Caricetum elatae*

Infolge des sanfteren Gefälles stehen den einzelnen Pflanzengesellschaften breitere Zonen zur Verfügung als im tiefer eingefurchten Altarmlauf. In der floristischen Zusammensetzung der einzelnen Zonen zeigt sich daher auch keine so scharfe Differenziertheit wie auf dem Mustergebiet 1.

Aus den angeführten Pflanzengesellschaften ist zu ersehen, dass die durch Bodenfeuchtigkeit und Bodentyp bedingten Zonationsverhältnisse bzw. die der entsprechenden Pflanzengesellschaften genau die gleichen sind wie im östlichen Teil dieses toten Armes; dass eine regelmässige, zwangsläufige Wiederholung vorliegt, mit der einzigen Ausnahme, dass zwischen dem *Caricetum vulpinae* und dem wiesenartigen *Caricetum elatae* auch noch *Caricetum acutiformis* vorkommt. Andererseits entfällt — wegen der fortgeschrittenen Verlandungsprozesse — *Scirpo-Phragmitetum*.

Bodenverhältnisse des Altarms von »Lakócsa«

In den toten Armen findet man den Verlandungs- und Wasserverhältnissen entsprechend die Zonation verschiedener Bodentypen. Die Sohlenaufladung beginnt mit Sand — zuallererst von grober, danach von feiner Körnung —; als nächstes setzt sich der Schwebestoff, m. a. W. der Schlamm. Die Drau führt silikatreichen Schlamm, in ihrem Schwebstoff ist kein oder nur wenig kohlensaures Kalk enthalten, und ist chemisch nicht sauer. Auf den stagnierenden Wasserflächen, in Altarmteichen kommt es allmählich zur Anhäufung von organischen Stoffen, während auf dem die toten Arme umrandenden Landstrich die Wiesenböden (zum Teil alluviale bzw. Auböden) erscheinen. In den tieferen Lagen, unter den *Magnocaricion*-Verbänden — dort, wo die durch den hohen Grundwasserspiegel und die periodische Wasserbedeckung bewirkten anaeroben Bedingungen einen erhöhten Anteil an organischen Substanzen (über 10%) herbeiführen — findet man die für sumpfige Wiesenböden charakteristischen Profile.

Im bereits verlandeten Mittelteil der toten Arme, wo sich der Anteil an organischen Stoffen auf 40 bis 50% beläuft, lässt sich der Bodentyp schon unter die Moorböden einreihen.

Es versteht sich von selbst, dass alle diese Bodentypen voneinander nicht scharf getrennt werden können, vielmehr zeigen sie in ihrer Beschaffenheit stufenweise Übergänge.

Im östlichen Lauf des Lakócsaer toten Armes, wo es noch einen mit Röhricht und Rohrkolben bedeckten Altarmteich gibt, kann lediglich von subaquatischem Rohboden, von einem Typ des sog. Protopedon — dem eutrophen Gyttja — gesprochen werden.

Über die physikalischen und chemischen Eigenschaften der wichtigeren Bodentypen des Mustergebietes geben die Angaben der Tafeln 3, 4, 5, 6 Aufschluss.

Veränderlichkeit der Bodenfaktoren in den Pflanzengesellschaften des östlichen Laufes des toten Armes von »Lakócsa«

Zur Bestimmung der Bodentypgrenzen bzw. zur Ermittlung des Veränderungsmasses der verschiedentlichen Bodenfaktoren dient die sog. Transektmethode, wobei in Abständen von je 1 m aus dem Bodenhorizont 0—20 cm Proben genommen werden. Die Bestimmung der Bodentypen erfolgte durch Profilerschliessung.

Die verschiedenen Bodeneigenschaften und parallel dazu die Pflanzengesellschaften ändern sich nach Massgabe der Feuchtigkeitsverhältnisse des Bodens bzw. den Bodentyps entsprechend (vgl. Abb. 6).

Die Pflanzengesellschaften sowie deren Zonen lassen die in den verschiedenen Bodenfaktoren eingetretenen Änderungen, die bodenökologischen Unterschiedlichkeiten gut erkennen.

Die Assoziationen *Arrhenatheretum elatioris* und *Festucetum pratensis* kommen auf alluvialem Wiesenboden, *Caricetum vulpinae* auf moorigem Wiesenboden, *Caricetum elatae* hingegen auf Moorboden vor. *Scirpo-Phragmitetum typhetosum* ist in Altarmteichen heimisch, auf Protopedon-Sediment.

Im Bildungsprozess der verschiedenen Bodenfaktoren spielt u. a. das Grundwasser bzw. der Feuchtigkeitsgehalt des Bodens eine wichtige Rolle.

Zur Zeit der Probennahme (am 24. Mai 1971) hatte der Boden der einzelnen Pflanzengesellschaften die folgenden Feuchtigkeitswerte (je Bestand Durchschnittswert von 25 Stichprobenentnahmen, im Horizont 0—20 cm).

Arrhenatheretum elatioris	17,9%
Festucetum pratensis	28,4%
Caricetum vulpinae	43,0%
Caricetum elatae	100,0%*

Parallel zum Anstieg des Bodenfeuchtigkeitsgehalts nimmt auch die Anaerobie zu, was wiederum infolge der verlängerten Dekompositionsprozesse eine Zunahme der organischen Stoffe im Boden herbeiführt (vgl. Abb. 6).

Die Humusqualität (Q-Wert) ist im Boden von *Festucetum pratensis* am günstigsten.

Der durchschnittliche pH-Wert beträgt im *Arrhenatherateum*-Boden als Folge der einstigen Bewaldung 5,8, während er bei den übrigen Assoziationen über 6 liegt. Für den A-Horizont der Böden von *Arrhenatheretum* und *Festucetum pratensis* dürfte man an Hand der pH-Werte auf eine mässige Auslaugung schliessen. Es ist anzunehmen, dass bei der oberflächlichen Auslaugung der von uns untersuchten Wiesenböden nebst der auslaugenden Wirkung des hoch anstehenden Grundwassers (vgl. STEFANOVITS 1968) auch der Auslaugungseffekt des gewesenen Waldes mit im Spiele war.

Wie die Bodenprofiluntersuchungen zeigen (vgl. Tafel 3, 4), beläuft sich der Tongehalt des Oberbodens auf etwa 25%; das Verhältnis der abschlämmbaren Teile ist mehr als 50%. Auf Grund der Werte der Schlämmanalyse (Fraktionsanalyse), der Hygroskopizität (hy) sowie

* Bis zu 100%-Wasserkapazität gesättiger Boden.

Tafel 3

Mittelmässig humushaltiger alluvialer Wiesenboden im Bestand Festucetum pratensis von Lakócsa, östl. Lauf des toten Armes
Probenentnahmestelle 1. Grube I

Genetische Horizonte	A			A/G	G	
Probenentnahme, cm	0–30	30–60	60–80	80–120	120–150	150–180
Grundmassdaten						
pH im Wasser	6,5	6,6	6,9	6,9	6,9	6,9
in n KCl	6,3	6,3	6,4	6,4	6,6	6,6
y_1	3,2	3,2	1,8	1,1	0,6	0,6
$CaCO_3$ %	.	.	.	0,7	0,3	0,1
hy	3,6	2,0	1,3	0,5	0,5	0,5
Humus %	6,1	4,4	1,5	.	.	.
Q	1,522	1,822	.	.	.	.
N %	0,348	0,236	0,108	.	.	.
NH_3-N mg/100 g	0,17	0,10	Sp.	.	.	.
NO_3-N mg/100 g	0,45	0,38	0,16	.	.	.
K_2O mg/100 g	8,6	6,1	3,9	3,8	3,8	2,7
P_2O_5 mg/100 g	5,4	17,0	63,4	88,0	70,4	69,2
Mechanische Zusammensetzung						
0,002 >	24,90	35,00	21,50	10,90	5,00	5,70
0,002—0,02	30,60	38,10	57,65	68,40	75,90	68,00
0,02 —0,2	43,80	26,70	20,60	18,00	10,70	9,70
< 0,2	0,70	0,20	0,25	2,70	8,40	16,60
Austauschbare Kationen						
Ca mval/100 g	30,31	28,72	15,00	5,00	2,11	4,00
Mg mval/100 g	9,57	6,12	4,67	4,19	2,62	2,54
K mval/100 g	0,27	0,23	0,13	0,15	0,16	0,11
Na mval/100 g	0,38	0,32	0,21	0,08	0,06	0,06
S mval/100 g	40,53	35,39	20,01	9,42	4,95	6,71
T mval/100 g	53,02	50,00	25,70	10,77	9,65	9,48
T-S	12,49	14,61	5,69	1,35	4,70	2,77
V %	76,44	70,78	77,85	87,46	51,29	70,78
Ca S %	74,78	81,15	74,96	53,07	42,62	59,61
Ma S %	23,61	17,29	23,33	44,47	52,92	37,85
K S %	0,66	0,64	0,64	1,59	3,23	1,63
Na S %	0,95	0,92	1,07	0,87	1,23	0,91

Tafel 4

Sumpfiger Wiesenboden im Bestand von Caricetum elatae Lakócsa, östl. Lauf des toten Armes
Probenentnahmestelle 1, Grube II

Genetische Horizonte	A				G		
Probenentnahme, cm	0–30	30–60	60–90	90–120	120–150	150–180	180–210
Grundmassdaten							
pH in Wasser	5,8	5,9	6,0	6,1	6,3	6,9	7,2
in n KCl	5,6	5,7	5,8	5,8	6,1	6,5	6,7
y_1	14,4	9,2	8,2	4,8	5,1	1,5	0,7
$CaCO_3$ %	.	.	.	.	.	1,5	6,6
hy	5,9	4,8	3,1	1,8	2,1	0,8	0,5
Humus %	16,5	13,4	8,7	4,3	4,4	0,7	0,5
Q	0,857	1,000	.	.	.	.	.
N %	0,824	0,576	0,328	0,184	.	.	.
NH_3-N mg/100 g	0,32	.	0,14	0,21	.	.	.
NO_3-N mg/100 g	0,75	.	0,80	0,30	.	.	.
K_2O mg/100 g	10,0	8,2	4,6	5,7	7,0	4,0	4,5
P_2O_5 mg/100 g	4,7	.	32,0	54,9	54,9	54,2	3,0
Mechanische Zusammensetzung							
0,002>	29,60	33,10	20,40	21,30	27,50	14,10	10,70
0,002—0,02	37,95	36,30	48,45	51,50	44,50	60,90	67,10
0,02 —0,2	28,90	28,70	29,70	25,80	26,90	19,20	20,90
<0,2	3,55	1,90	1,45	1,40	1,10	5,80	1,30
Austauschbare Kationen							
Ca mval/100 g	48,40	43,61	30,85	19,42	21,71	4,88	6,11
Mg mval/100 g	9,57	8,93	5,72	4,91	5,00	3,43	4,35
K mval/100 g	0,31	0,24	0,16	0,15	0,24	0,16	0,16
Na mval/100 g	0,65	0,51	0,32	0,22	0,28	0,15	0,10
S mval/100 g	58,93	53,29	37,05	24,70	27,23	8,62	10,72
T mval/100 g	78,93	76,31	53,57	44,78	46,42	22,78	21,65
T-S	20,00	23,02	16,52	20,08	19,19	14,26	10,93
V %	74,66	69,83	69,16	55,15	58,66	37,67	49,51
Ca S %	82,13	81,83	83,26	78,62	79,72	56,61	56,99
Mg S %	16,23	16,75	15,43	19,87	18,36	39,79	40,57
K S %	0,52	0,55	0,43	0,61	0,88	1,85	1,49
Na S %	1,12	0,87	0,88	0,90	1,04	1,75	0,95

Tafel 5

Signifikante Differenzen der Mittelwerte des Bodenfaktoren in den Pflanzengesellschaften des östlichen Laufes des toten Arms von Lakócsa

	2. *Festucetum pratensis*		3. *Caricetum vulpinae*	4. *Caritatum elatae*	5. *Scirpo-Phragmitetum*
	x̄	Wiesenboden	Moorwiesenboden		Eutrophe Gyttja
1. *Arrhenatheretum elatioris*					
pH im Wasser	5,84	NS	(+)	(+)	(+)
y_1	6,90	NS	NS	(+)	(+)
hy	2,37	NS	+	++	+++
Humus %	4,75	+	+++	+++	++
N %	0,267	+	+++	+++	+++
NH_3-N mg/100 g	0,22	NS	NS	++	+
NO_3-N mg/100 g	0,39	NS	(+)	+++	+
P_2O_5 mg/100 g	21,00	+	+	+	+
K_2O mg/100 g	8,58	(+)	+	+++	+++
adsorbiertes Ca mval/100 g	20,72	++	+++	+++	+++
S mval/100 g	26,09	++	+++	+++	+++
T mval/100 g	41,86	++	+++	+++	+++
V %	61,98	++	+	+	NS
2. *Festucetum pratensis*					
pH im Wasser	6,22		NS	NS	NS
y_1	5,96		++	+	++
hy	2,77		+++	+++	+++
Humus %	7,49		+++	+++	++
N %	0,382		+++	+++	+++
NH_3-N mg/100 g	0,25		NS	+	(+)
NO_3-N mg/100 g	0,45		NS	+++	+
P_2O_5 mg/100 g	6,70		(+)	NS	(+)
K_2O mg/100 g	9,42		NS	+++	+++
adsorbiertes Ca mval/100 g	30,92		++	++	+
S mval/100 g	37,23		++	++	++
T mval/100 g	48,95		++	+++	+++
V %	75,94		NS	NS	+++
3. *Caricetum vulpinae*					
pH im Wasser	6,24			NS	NS
y_1	6,96			(+)	++
hy	3,73			++	(+)
Humus %	11,53			++	++
N %	0,548			++	(+)
NH_3-N mg/100 g	0,29			+	(+)
NO_3-N mg/100 g	0,53			++	(+)

Tafel 5 (Cont.)

	2. *Festucetum pratensis*	3. *Caricetum vulpinae*	4. *Caricetum elatae*	5. *Scirpo-Phragmitetum*
	Wiesenboden	Moorwiesenboden		eutrophe Gyttja
P_2O_5 mg/100 g	4,20		+	+++
K_2O mg/100 g	9,91		++	++
adsorbiertes Ca mval/100 g	39,11		NS	(+)
S mval/100 g	47,62		(+)	(+)
T mval/100 g	64,02		+	NS
V %	74,97		NS	(+)
4. *Caricetum elatae*				
pH im Wasser	6,37			NS
y_1	11,32			NS
hy	5,97			NS
Humus %	21,66			NS
N %	0,970			(+)
NH_3-N mg/100 g	0,43			NS
NO_3-N mg/100 g	6,05			++
P_2O_5 mg/100 g	6,90			(+)
K_2O mg/100 g	16,10			(+)
adsorbiertes Ca mval/100 g	44,17			(+)
S mval/100 g	54,51			(+)
T mval/100 g	75,71			(+)
V %	71,88			+
5. *Scirpo-Phragmitetum*				
pH im Wasser	6,32			
y_1	9,44			
hy	5,68			
Humus %	16,47			
N%	0,640			
NH_3-N mg/100 g	0,40			
NO_3-N mg/100 g	0,97			
P_2O_5 mg/100 g	8,70			
K_2O mg/100 g	20,05			
adsorbiertes Ca mval/100 g	36,71			
S mval/100 g	44,78			
T mval/100 g	69,16			
V %	64,84			

NS: zwischen den beiden Mittelwerten besteht kein signifikanter Unterschied
(+): zwischen den beiden Mittelwerten besteht 10% signifikanter Unterschied
+: zwischen den beiden Mittelwerten besteht 5% signifikanter Unterschied
++: zwischen den beiden Mittelwerten besteht 1% signifikanter Unterschied
+++: zwischen den beiden Mittelwerten besteht 0,1% signifikanter Unterschied

Tafel 6

In Oberflächenhöhe karbonathaltiger, seicht humusreicher Wiesenboden im Bestand von Arrhenatheretum elatioris Lakócsa, westl. Lauf des toten Armes
Probenentnahmestelle 2, Grube I

Genetische Horizonte	A	B			G		
Probenentnahme, cm	0–20	20–50	50–70	70–95	95–110	110–130	130–160
Grundmassdaten							
pH im Wasser	5,6	7,0	7,5	7,4	7,5	7,7	7,4
in n KCl	5,3	6,8	7,2	7,2	7,3	7,4	7,3
y_1	6,8	1,1	0,5	0,5	0,5	0,5	0,5
$CaCO_3$ %	0,0	2,0	17,6	3,5	6,0	6,5	0,9
hy							
Kapillare Wasserhebung							
in mm nach 5 Stunden	105	130	135	130	170	175	295
" 20 "	205	265	265	270	310	325	405
" 100 "	395	550	500	430	685	605	885
Humus %	3,3	1,6	0,4	0,3	.	.	.
Q	0,965	.	.	.	.	.	.
N %	0,200	0,084	0,040	.	.	.	.
NH_3-N mg/100 g	0,25	0,12	.	.	.	.	.
NO_3-N mg/100 g	0,20	0,20	0,13	.	.	.	.
K_2O mg/100 g	10,0	7,6	5,4	7,0	5,4	6,6	5,3
P_2O_5 mg/100 g	17,6	3,0	Sp.	0,0	0,0	0,0	0,0
Mechanische Zusammensetzung							
0,002>	32,10	34,20	27,30	30,10	19,00	17,00	7,70
0,002—0,02	33,05	27,20	19,60	32,15	47,75	49,95	69,65
0,02 —0,2	33,10	37,90	52,30	36,50	30,90	31,30	20,60
<0,2	1,75	0,70	0,80	1,25	2,35	1,75	2,05
Austauschbare Kationen							
Ca mval/100 g	12,71	22,34	21,27	21,14	19,42	21,14	7,11
Mg mval/100 g	6,29	5,80	5,16	5,16	5,08	5,00	4,00
K mval/100 g	0,35	0,21	0,16	0,23	0,22	0,26	0,22
Na mval/100 g	0,12	0,13	0,15	0,18	0,18	0,18	0,09
S mval/100 g	24,47	28,48	26,74	26,71	24,90	26,58	11,42
T mval/100 g	44,50	42,30	24,47	24,82	24,64	24,28	22,00
T-S	20,03	13,82	.	.	.	.	10,58
V %	54,98	67,32	100	100	100	100	51,90
Ca S %	72,37	78,44	79,54	79,14	77,99	79,53	62,25
Mg S %	25,70	20,36	19,29	19,31	20,40	18,81	35,02
K S %	1,43	0,73	0,59	0,86	0,88	0,97	1,92
Na S %	0,50	0,47	0,58	0,69	0,73	0,69	0,81

Tafel 7

Sumpfiger Wiesenboden im Bestand Caricetum acutiformis Lakócsa, westl. Lauf des toten Armes
Probenentnahmestelle 2, Grube II

Genetische Horizonte	A				C	
Probenentnahme, cm	0–20	20–40	40–60	60–90	90–110	110–130
Grundmassdaten						
pH im Wasser	6,8	6,6	6,8	6,7	6,6	7,4
in n KCl	6,4	6,3	6,4	6,4	6,3	7,2
y_1	2,0	2,5	1,7	2,6	1,2	0,6
$CaCO_3$ %	Sp.	Sp.	Sp.	Sp.	Sp.	2,1
hy	4,5	3,4	3,0	2,1	1,0	1,0
Kapillare Wasserhebung in mm						
nach 5 Stunden	165	60	70	105	275	385
" 20 "	265	120	140	200	370	515
" 100 "	335	215	280	380	470	635
Humus %	12,2	6,5	3,2	5,3	.	.
Q	4,085	4,459	.	.	.	.
N %	0,668	0,404	0,164	.	.	.
NH_3-N mg/100 g	0,30	0,14	0,0	.	.	.
NO_3-N mg/100 g	0,90	0,24	0,13	0,24	.	.
K_2O mg/100 g	20,5	22,1	20,5	16,6	4,1	3,9
P_2O_5 mg/100 g	2,0	9,4	4,2	18,7	33,3	6,5
Mechanische Zusammensetzung						
0,002 >	30,20	39,60	46,40	32,30	4,60	4,00
0,002–0,02	30,50	22,40	16,00	29,65	56,15	68,40
0,02 –0,2	35,70	36,60	36,50	32,90	6,00	5,00
< 0,2	3,60	1,40	1,10	5,15	33,25	22,60
Austauschbare Kationen						
Ca mval/100 g	46,80	32,44	27,65	25,53	5,00	5,00
Mg mval/100 g	6,61	6,37	6,45	6,29	3,35	3,19
K mval/100 g	0,73	0,82	0,73	0,59	0,16	0,24
Na mval/100 g	0,41	0,27	0,21	0,19	0,03	0,03
S mval/100 g	54,55	39,93	35,04	32,60	8,54	8,46
T mval/100 g	73,03	68,77	52,19	52,19	10,43	10,94
T-S	18,48	28,84	17,15	19,59	3,89	2,48
V %	74,69	58,06	67,13	62,46	71,88	77,33
Ca S %	85,79	81,24	78,90	78,31	58,54	59,10
Mg S %	12,11	15,95	18,40	19,29	39,28	37,70
K S %	1,33	2,05	2,08	1,81	1,87	2,83
Na S %	0,77	0,76	0,62	0,59	0,37	0,37

der kapillaren Grundwassererhöhung (Tafel 2) qualifiziert sich die physikalische Bodenart als Lehm bzw. toniger Lehm.

Bei moorigem Wiesenboden bzw. Moorboden übernimmt schon der organische Stoffgehalt die ausschlaggebende Rolle bei der Gestaltung zahlreicher Bodenfaktoren. So ist vom Wiesenboden über dem moorigen Wiesenboden bis zum Moorboden (vgl. Abb. 6) ein Anwachsen der Hygroskopizität und des Adsorptionsvermögens zu verzeichnen. Parallel zur Zunahme des Adsorptionsvermögens vermehrt sich die Gesamtstickstoffmenge (wovon die Pflanzen einen ziemlich grossen Anteil nicht aufnehmen können), sowie der Gehalt an NH_3-N und NO_3-N.

Der leicht aufnehmbare K_2O-Gehalt kommt im Boden der Gesellschaften *Arrhenatheretum*, *Festucetum pratensis* und *Caricetum vulpinae* in einer Menge von 8—9 mg/100 g vor. Mit bedeutenderen Mengen (16—20 mg/100 g) ist er im Boden von *Caricetum elatae* und im Protopedon von Rohrkolbengesellschaften vertreten. Vom Wiesenheu wird in ansehnlicher Menge K_2O angehäuft, das aber durchs Mähen regelmässig wieder dem Boden entzogen wird, somit kommt es zu einer allmählichen Verarmung des Bodens an leicht aufnehmbarem K_2O.

Die ungemähte Streu von *Caricetum elatae* und *Scirpo-Phragmitetum typhetosum* bleibt gänzlich an Ort und Stelle, wodurch das K_2O in den Boden zurückgelangt.

Das leicht aufgenommene P_2O_5 ist in der Randzone der toten Arme (im Boden der *Arrhenatheretum*-Gesellschaft) am stärksten vertreten, was am wahrscheinlichsten der einstigen Walddecke bzw. der phosphorreichen Streu des *Querco-Carpinetum* und *Fraxino pannonicae-Ulmetum* zuzuschreiben ist. Der hohe Phosphorgehalt der unteren Bodenhorizonte (vgl. Tafel 3, 4) dürfte von den einstigen Überschwemmungen, Inundationen herrühren.

Wie aus der Aufstellung der signifikanten Mittelwertdifferenzen der einzelnen Bodenfaktoren erhellt (Tafel 5; t-Rechnung, vgl. Sváb 1967), sind die einzelnen Pflanzengesellschaften, Zonen bodenökologisch sehr scharf differenziert.

Die unter Laborbedingungen untersuchte Nitrifikationsdynamik zeigt vom *Arrhenatheretum*-Boden bis zum Boden von *Caricetum elatae* einen gleichmässigen Anstieg (Tafel 9). Die Ursache liegt darin, dass der adsorbierte Ca-Gehalt die Nitrifikationsdynamik güngstig beeinflusst.

Auf moorigem Wiesenboden und auf Moorboden ist — unter natürlichen Voraussetzungen — infolge der vorherrschenden anaeroben Umstände die Nitrifikation nicht so güngstig. Bei der unter Laborverhältnissen erfolgten künstlichen Bodenreife spielt sich ein ähnlicher Prozess ab wie in der Natur beim Torfstechen, bei der Urbarmachung von Moorböden, wo der organisch gebundene Stickstoff rapid aufgeschlossen wird, und stickstoffliebendes Unkraut massenhaft aus dem Boden schiesst.

Die Veränderlichkeit der Bodenfaktoren in den Pflanzengesellschaften des westlichen Altarmlaufs von »Lakócsa«

Den Zonationsverhältnissen entsprechend wurden in 6 Beständen von 5 Pflanzengesellschaften Transektuntersuchungen der Bodenfaktoren vorgenommen (Abb. 7, 8).

Der *Arrhenatheretum elatioris*- und der *Festucetum pratensis*-Bestand der supralitoralen Zone der Landrücken und des toten Armes kommt auf Wiesenboden; *Caricetum vulpinae* und *Caricetum acutiformis* auf moorigem Wiesenboden, *Caricetum elatae* auf Moorboden vor.

Gerade zur Zeit der Untersuchungen (am 25. Mai 1971) zeigten die Bodenfeuchtigkeitswerte der verschiedenen Pflanzengesellschaften eine allmähliche Zunahme in der Richtung gegen die Zentralzone (vgl. Abb. 8).

Im östlichen und im westlichen Teil des Lakócsaer toten Armes wiederholen sich den Wasser- und Bodenverhältnisse gemäss dieselben Pflanzengesellschaften, und die einzelnen Bodenfaktoren verändern sich im gleichen Mass. Auf dem Rücken und in der supralitoralen Zone des toten Armes — wo man aufs Vorkommen von einstigem *Querco robori-Carpinetum* bzw. *Fraxino pannonicae-Quercetum* schliessen kann — ist der pH-Wert des Oberbodens 5,6–5,8 (vgl. Tafel 6).

Die chemische Reaktion des Oberbodens wird in Richtung auf die Mittelzone des toten Armes zu immer stärker (Tafel 7).

Auf Grund der mechanischen Beschaffenheit sind hier die Wiesenböden reicher an Ton, auch ist der abschlämmbare Anteil etwas höher als im östlichen Lauf des toten Armes. Im westlichen Teil floss die damalige Drau zwischen sanfter abfallenden Uferabschnitten, in einem breiteren Bett, und infolge der morphologischen Faktoren bzw. der abgebremsten Strömung wurden in den Randzonen grössere Mengen von Schwebstoffen bzw. Ton abgesetzt.

Die tonreichere Zusammensetzung der Randzone wird — ausser der mechanischen Beschaffenheit — auch durch die Werte der Hygroskopizität (hy) und der kapillaren Wasserhebung erhärtet (Abb. 8).

Im Boden der *Magnocaricion*-Wiesen erscheint in geringeren Mengen auch $CaCO_3$.

Die kapillaren Wasserhebungswerte der Moorböden werden u. a. auch durch den Organstoffgehalt des Bodens beeinflusst (vgl. DI GLÉRIA, J.—KLIMES-SZMIK, A.—DVORACSEK, M. 1957) (Tafel 8).

Der zentralen Zone des toten Armes zu, im gleichen Sinne wie der steigende Organstoffgehalt, wächst auch das Adsorptionsvermögen der Böden (der T-Wert), die Menge der adsorbierten Kationen (S-Wert) und die Sättigung des Bodens (V %).

Am günstigsten gestaltet sich die Humusform in den Böden von *Festucetum pratensis* und *Caricetum vulpinae*, wo der Wechsel von anaeroben und aeroben Verhältnissen mit einem vermehrten Gehalt an Ca einhergeht.

In Hinsicht des leichtlöslichen K_2O gibt es zwischen den Böden der Pflanzengesellschaften keine so scharfen Unterschiede wie im östlichen Totarmlauf; wohl darum, weil beide Wiesen — so auch das auwiesenartige, bültige Seggenland — gleicherweise gemäht werden.

Die in Bodenfaktoren messbaren signifikanten Differenzen zwischen den verschiedenen Pflanzengesellschaften sind datenmässig auf Tafel 10 zusammengestellt.

Aus den Laboruntersuchungen über die Nitrifikation geht hervor (vgl. Tafel 9), dass die während 28 Tage im Boden anfallende NO_3-N-Menge von *Arrhenatheretum* bis zur *Festucetum pratensis*-Zone ein Wachstum zeigt, aber auch im Boden der *Magnocaricion*-Verbände waren noch hohe Werte zu messen.

Tafel 8

Kapillare Wasserhebung der Böden im toten Arm von Lakócsa

Pflanzengesellschaft	Kapillare Wasserhebung in mm nach		
	5	20	100
	Stunden		
Östlicher Lauf des toten Armes			
1. *Arrhenatheretum elatioris*	128	215	349
2. *Festucetum pratensis*	105	173	274
Westlicher Lauf des toten Armes			
1. *Arrhenatheretum elatioris*	94	173	307
2. *Arrhenatheretum elatioris*	94	162	266
3. *Festucetum pratensis*	96	152	231
4. *Caricetum acutiformis*	111	178	266
5. *Caricetum acutiformis*	80	113	176
6. *Caricetum elatae*	64	85	131

1 5 10 15 20 25 30 35 40 45 50 55 60
Arrhenatheretum elatioris
Festucetum pratensis
Caricetum vulpinae
Caricetum acutiformis
Caricetum elatae
Feuchtigkeitsgehalt des Bodens am 25.5.1971.
Kapillare Wasserhebung in mm nach 5
20
100 Stunden
torfiger Boden
Mechanische Zusammensetzung
0,002
0,002-0,02
0,02-0,2
0,2
hy
pH im Wasser
y1
T-S mval/100 g
CaCO3 %
Humus (organische Substanzen) %
Q (Humus-stabilitätswert)

Abb. 8. Die Änderungen der Bodenfaktoren in den Pflanzengesellschaften des Westlaufes des toten Armes von »Lakócsa«

Tafel 9

Nitrifikationsdynamik der Böden im toten Arm von Lakócsa, auf Grund von Bodenreifungsuntersuchungen

Pflanzengesellschaft	Unter Zugabe von NO_3-N mg/100 g 0,1% $(NH_4)_2SO_4$				Unter Zugabe von NO_3-N mg/100 g 0,1% $(NH_4)_2SO_4$ + 1% $CaCO_3$	NH_3-N mg/100 g urspr. Boden	NO_3-N urspr. Boden
	nach 7 Tagen	nach 14 Tagen	nach 21 Tagen	nach 28 Tagen	nach 28 Tagen	nach 28 Tagen	nach 28 Tagen
Östlicher Lauf des toten Armes von Lakócsa							
1. *Arrhenatheretum elatioris*	1,7	4,0	6,7	6,8	10,7	0	3,7
2. *Festucetum pratensis*	3,2	5,9	10,3	10,4	11,8	0	6,2
3. *Caricetum vulpinae*	4,0	7,9	12,8	13,0	14,1	0	7,7
4. *Caricetum elatae*	7,4	12,8	20,8	21,0	21,6	0	13,7
5. *Scirpo-Phragmitetum typhetosum*	2,5	7,7	12,5	13,2	14,8	0	9,6
Westlicher Lauf des toten Armes von Lakócsa							
1. *Arrhenatheretum elatioris*	2,4	4,8	7,6	7,8	8,3	0	2,8
2. *Arrhenatheretum elatioris*	2,6	4,3	7,4	7,6	12,2	0	4,3
3. *Festucetum pratensis*	6,5	13,4	19,2	19,4	18,4	0	11,8
4. *Caricetum vulpinae*	2,3	14,4	16,3	17,0	15,0	0	12,5
5. *Caricetum acutiformis*	7,0	11,2	13,8	14,5	14,3	0,6	11,8
6. *Caricetum elatae*	7,7	10,5	12,5	13,0	12,3	0,6	10,3

Tafel 10

Signifikante Differenzen der Mittelwerte der Bodenfaktoren in den Pflanzengesellschaften des westlichen Laufes des toten Armes von Lakócsa

	$\bar{x}$	2. *Arrhenatheretum brometosum*	3. *Festucetum pratensis*	4. *Caricetum vulpinae*	5. *Caricetum acutiformis*	6. *Caricetum elatae*
		Wiesenboden		Sumpfiger Wiesenboden	Moorboden	
1. *Arrhenatheretum elatioris*						
pH im Wasser	5,86	NS	+++	+++	+++	+++
y_1	6,13	+	+++	+++	+	+++
hy	3,02	(+)	+++	+++	+++	+++
N %	0,25$_7$	+++	+++	+++	+++	+++
NO_3-N mg/100 g	0,36	NS	+	(+)	NS	+
N_3N-N mg/100 g	0,48	++	++	++	+++	+++
P_2O_5 mg/100 g	18,70	+	+++	+++	+++	+++
K_2O mg/100 g	13,70	++	+	+	+	+
adsorbiertes Ca mval/100 g	23,41	NS	+++	+++	+++	+++
S mval/100 g	29,29	NS	+++	+++	+++	+++
T mval/100 g	42,85	(+)	+++	+++	+++	+++
V %	68,42	NS	+++	+++	+++	+++
2. *Arrhenatheretum elatioris brometosum*						
pH im Wasser	5,70		+++	+++	+++	+++
y_1	8,05		+++	+++	++	+++
hy	2,87		+++	+++	+++	+++
Humus %	5,94		+++	+++	+++	+++
N %	0,234		+++	+++	+++	+++
NH_3-N mg/100 g	0,39		++	NS	NS	++
NO_3-N mg/100 g	0,76		++	+++	+++	+++
P_2O_5 mg/100 g	21,80		+++	+++	+++	+++
K_2O mg/100 g	19,91		NS	NS	(+)	+++
adsorbiertes Ca mval/100 g	23,04		+++	+++	+++	+++
S mval/100 g	28,86		+++	+++	+++	+++
T mval/100 g	43,92		+++	+++	+++	+++
V %	65,62		+++	+++	+++	+++
3. *Festucetum pratensis*						
pH im Wasser	6,62			+++	++	++
y_1	2,23			+	NS	NS
hy	4,78			+++	+++	+++
Humus %	11,02			+++	+++	+++
N %	0,600			+++	+++	+++
NH_3-N mg/100 g	0,24			NS	+	NS
NO_3-N mg/100 g	1,57			NS	+++	+++
P_2O_5 mg/100 g	6,70			++	+++	+++
K_2O mg/100 g	17,05			NS	NS	+++
adsorbiertes Ca mval/100 g	43,78			+++	+++	+++
S mval/100 g	51,40			+++	+++	+++
T mval/100 g	64,49			+++	+++	+++
V %	79,97			NS	+	++
4. *Caricetum vulpinae*						
pH im Wasser	7,31				(+)	NS
y_1	1,50				(+)	(+)

Tafel 10 (Cont.)

	$\bar{x}$	2. *Arrhenatheretum brometosum*	3. *Festucetum pratensis*	4. *Caricetum vulpinae*	5. *Caricetum acutiformis*	6. *Caricetum elatae*
		Wiesenboden		Sumpfiger Wiesenboden	Moorboden	
hy	6,70				NS	+++
Humus %	16,34				+++	+++
N %	0,901				+++	+++
NH_3-N mg/100 g	0,28				(+)	NS
NO_3-N mg/100 g	3,08				+	+++
P_2O_5 mg/100 g	1,50				+++	+++
K_2O mg/100 g	21,15				(+)	++
adsorbiertes Ca mval/100 g	67,22				++	+++
S mval/100 g	77,72				++	+++
T mval/100 g	93,98				++	+++
V %	83,15				NS	+
5. *Caricetum acutiformis*						
pH im Wasser	7,06					NS
y_1	3,23					NS
hy	6,78					+++
Humus %	21,35					+++
N %	1,114					+++
NH_3-N mg/100 g	0,36					+
NO_3-N mg/100 g	6,23					++
P_2O_5 mg/100 g	0,10					NS
K_2O mg/100 g	16,39					++
adsorbiertes Ca mval/100 g	77,02					+++
S mval/100 g	85,36					+++
T mval/100 g	100,14					++
V %	85,46					NS
9. *Caricetum elatae*						
pH im Wasser	7,08					
y_1	2,76					
hy	8,60					
Humus %	46,26					
N %	1,408					
NH_3-N mg/100 g	0,27					
NO_3-N mg/100 g	11,44					
P_2O_5 mg/100 g	0,10					
K_2O mg/100 g	11,34					
adsorbiertes Ca mval/100 g	83,09					
S mval/100 g	98,59					
T mval/100 g	110,43					
V %	89,26					

NS: zwischen den beiden Mittelwerten besteht kein signifikanter Unterschied
(+): zwischen den beiden Mittelwerten besteht 10% signifikanter Unterschied
+: zwischen den beiden Mittelwerten besteht 5% signifikanter Unterschied
++: zwischen den beiden Mittelwerten besteht 1% signifikanter Unterschied
+++: zwischen den beiden Mittelwerten besteht 0,1% signifikanter Unterschied

Zusammenfassung der Untersuchungsergebnisse

1. Im Inundationsgebiet der Drau befindet sich der (im Sinne der Stromrichtung) obere Lauf der toten Arme in einem mehr fortgeschrittenen Stadium der Verlandung bzw. der Sukzessionsfolge als der Unterlauf.

2. In den eutrophen Altarmen vom Wassertype $Ca(HCO_3)_2$ des Inundationsgebietes der Drau kommen den hydrologischen Verhältnissen entspre-
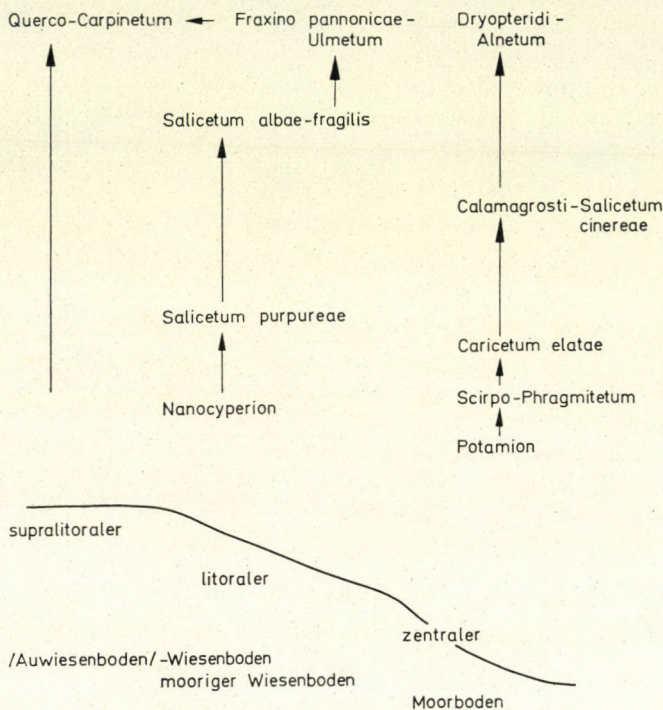
Abb. 9. Sukzessionsschema der toten Arme im Überschwemmungsgebiet der Drau

chend dieselben Bodentypen und Pflanzengesellschaften in regelmässiger Wiederholung vor.

Je nach den morphologischen Verhältnissen ist für die supralitorale und litorale Zone, für deren Entwicklung — dem Alluvialgut der einstigen Drau entsprechend — die sandige, schlammige, minerogene Verlandung kennzeichnend. Auf dem nährstoffreichen Schlammboden fassten primär zunächst die *Nanocyperion*-Elemente und *Salix purpurea* Fuss (Abb. 9). Dieser Verlandungsprozess ist auch bei den gegenwärtig in Abschnürung befindlichen toten Armen der Drau im Gange. Auf dem alluviogenen Boden der supralitoralen und litoralen Zone spielen sich die Bildungsprozesse der Wiesen-

böden ab. Als abschliessende Assoziation kommen — durch die Grundwasserverhältnisse bedingt — Auwald oder Hainbuchen-Eichenwald (bzw. in solche übergehende Bestände) in Frage.

3. Für die zentrale Zone der toten Arme ist die organogene Sukzessionsserie bzw. ein solcher Verlandungsprozess charakteristisch; im Übergang zwischen der litoralen und der zentralen Zone ist mooriger Wiesenboden, im Zentralstück teilweise mit Moorboden sowie mit Moorwald als Abschlussgesellschaft.

Im Anfangsstadium des Verlandungsprozesses, in den jüngeren toten Armen — wo es im Zentrum teilweise noch offene, oder mit Laichkraut und Röhricht bedeckte wasserflächen, Altarmteiche gibt — findet man am Teichgrund den subaquatischen Rohboden, in der Form von eutrophem Gyttja.

4. Als Folgeerscheinung der morphologischen Entwicklung der toten Arme, sowie hydrologisch bedingt, ist eine charakteristische Zonation der Bodentypen anzutreffen, bei welcher die Bodentypen bzw. die einzelnen Bodeneigenschaften dem Gefälle der litoralen Zone entsprechend mehr oder weniger sukzessive Änderungen zeigen.

Zahlreiche Faktoren (geomorphologische Verhältnisse, Art der Alluvion, Grundwassertiefe, Verlandungsprozesse, vorhergehende Bewaldung, menschliche Kultureinflüsse, regelmässiges Mähen usw.) bewirken es in ihrer Gesamtheit, dass sich bei vielen Bodenfaktoren die quantitativen Verhältnisse in einem bestimmten Sinne ändern (Abb. 10). So z. B. erhöht sich der Organstoffgehalt des Bodens und wächst die Tiefe (die Mächtigkeit) des an organischen Substanzen reichen Horizonts von der supralitoralen Zone angefangen bis zur zentralen, u. zw. parallel zu den mit den Feuchtigkeitswerten zugleich erstarkenden anaeroben Bedingungen. Parallel zum organischen Stoffgehalt erfolgt auch eine Zunahme der damit positiv korrelierenden Faktoren wie Hygroskopizität, Adsorptionsvermögen, adsorbiertes Ca, Menge der adsorbierten Kationen, Sättigung des Bodens. Die Zunahme des pH-Wertes einerseits, die Abnahme der hydrolytischen Azidität anderseits stehen mit dem Anwachsen des adsorbierten Ca-Gehalts des Bodens im Zusammenhang.

Dem Zentrum hin ansteigender organischer Stoffgehalt bedeutet eine Verschlechterung der kapillaren Wasserhebung.

Für die Werte des adsorbierten Ca und des pH im Oberboden der supralitoralen und litoralen Zone ist die einstige Waldbedecktheit, die alkalisierende Wirkung des organischen Stoffgehaltes des Waldes massgebend, während in der zentralen Zone die biogenen Kalkkonkretionen eine massgebliche Rolle spielen.

Für die — quantitativ der supralitoralen Zone hin ansteigenden — Phosphorgehaltwerte des Oberbodens ist die einstige Walddecke, die phosphorreiche Streu massgebend. — Der Gehalt an dem leicht aufgenommenen K_2O wird entscheidend durch die menschlichen Kultureinwirkungen bestimmt. In den Wiesengesellschaften der regelmässig gemähten Supralitoral- bzw.
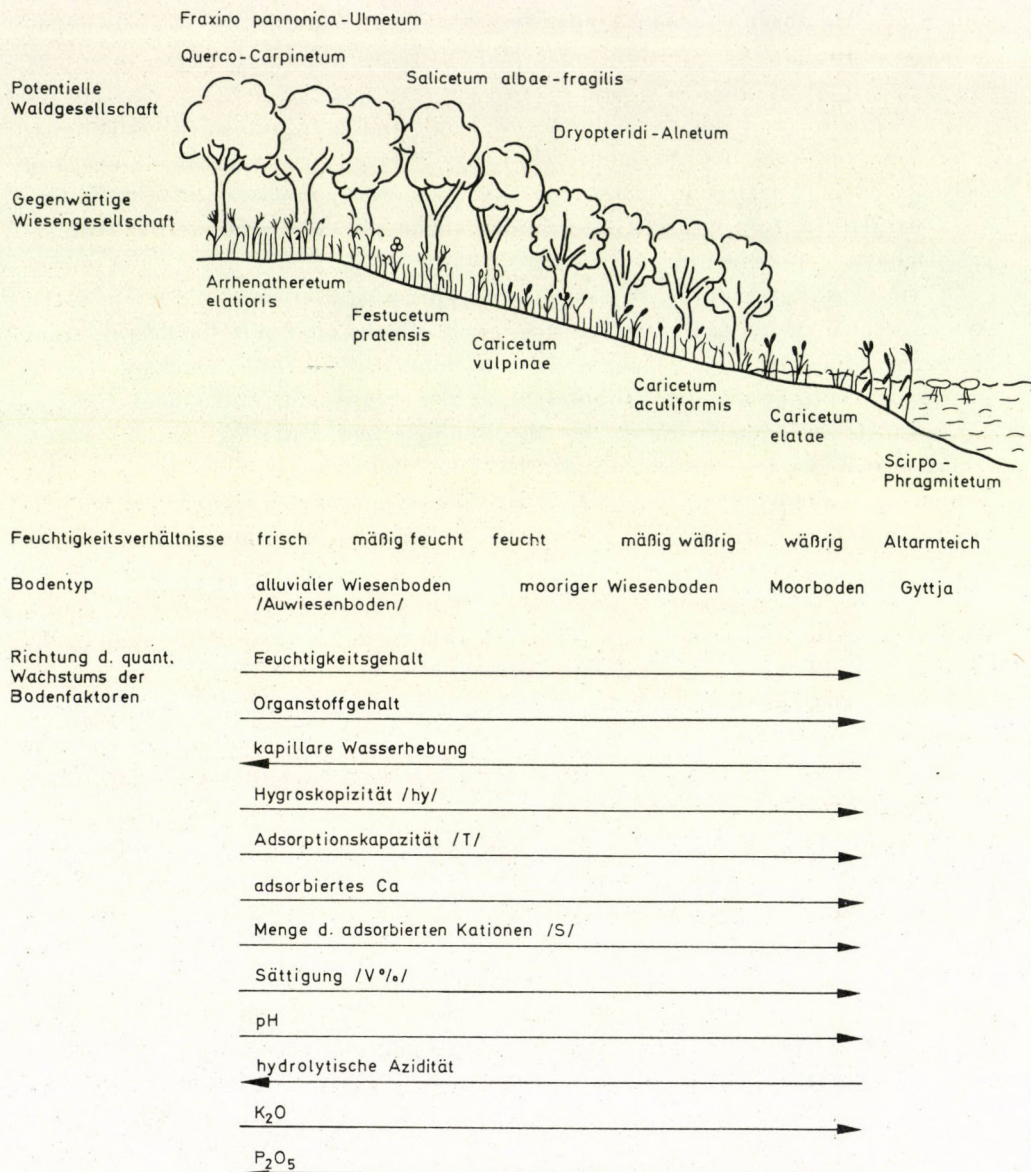
Abb. 10. Boden- und Vegetationszonation der toten Arme im Überschwemmungsgebiet der Drau, Richtung der quantitativen Zunahme der Bodenfaktoren

Litoralzone der Altarme werden ansehnliche Kaliummengen angehäuft, wodurch der Oberboden Jahr zu Jahr um eine bestimmte Menge Kalium ärmer wird.

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INFLORESCENCE ANATOMY AND FLORAL MORPHOLOGY OF AMARANTHUS LEUCOCARPUS S. WATS

By

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In *Amaranthus leucocarpus* the inflorescence is a raceme of dichasia. There is a regular reduction in number of flowers in a cluster. The maximum number of flowers in a cluster is nine and reduction continues in steps of seven to five and ultimately to three flowers representing three central flowers of three dichasia.

Introduction

It would be interesting to study the sequence of floral reduction in the inflorescence of *Amaranthaceae*. JOSHI and RAO (1934) have arrived at certain important conclusions regarding the morphology and the early history of the family *Amaranthaceae* from their studies on the floral vasculature of *Digeria arvensis*. BAKSHI (1952) has, however, pointed out that some of these conclusions at least do not appear to be warranted by facts. Besides, some of their observations also need confirmation. BAKSHI and CHHAJLANI (1954) published an excellent account of the floral anatomy of *Digeria arvensis*, *Pupalia lappacea*, *Achyranthus aspera* and *Gomphrena globosa*. RAO (1963) has indicated an interesting parallelism in the reduction of inflorescence in *Amaranthaceae*.

Material and methods

The seeds of *Amaranthus leucocarpus* S. WATS were obtained from the Plant Introduction Division of the Indian Agricultural Research Institute, New Delhi. The inflorescence at various stages were fixed in F. A. A. Usual procedure of dehydration and paraffin embedding were followed. Microtome sections were cut at 12 micron thickness and sections stained with safranin-anilin blue combination.

Observations

The organization of the inflorescence is apparently a spike which is axillary as well as terminal (Microphot. 1, 2). Each bract (Br. 1) on the main axis of the inflorescence subtends a short secondary spike, on which

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occur cymose clusters of flowers. The number of flowers in each cluster varies from nine (maximum number, Figs 1a, 2), five (Fig. 1c) to three (Fig. 1d). In the cluster with five flowers, the extreme lateral flowers appear abortive (Fig. 3). This leads to a cluster composed of either female or male flowers [aone or both male and female flowers. In case the cluster shows both male and female flowers the central flower is male and the lateral ones are female.

Inflorescence apex

The material fixed on 19 Sept., 1970, indicates an apex at the transition between the vegetative and reproductive phases. The apex shows no zonation, except two distinct tunica layers. The corpus is represented only by the central mother cells zone. The flanking zone and pith rib meristem show vacuolization which is more pronounced in the latter. This apex elongates considerably to form the inflorescence apex as has been observed in the material fixed on 21 and 22 Sept., 1970. The apex fixed on 21 Sept., shows the initiation of only a few axillary reproductive apices and in the one fixed on 22 Sept., 1970, there is formation of a considerable number of axillary reproductive apices The inflorescence apex is tapering with a convex tip. The inner of the two tunica layers shows periclinal division at the point of initiation of bracts. The first axillary shoot arises in the axil of the second bract from the apex. The development of this axillary shoot takes place in the same manner as that of the axillary bud which forms the vegetative bract. Each reproductive apex initiates the bract Br. 2 (Figs 3, 4), in the axil of which occurs cluster apex. The cluster apex in turn initiates bracts which subtend floral apices. Thus, there occur three categories of apices in addition to the main inflorescence apex: (1) the axillary apex which forms the reproductive shoot (2), the cluster apex (3), the floral apex (Fig. 3). All these apices show a similar organization to that of the main inflorescence apex, the difference being in size only. The inflorescence is thus a combination of both determinate and indeterminate types of apices. The procambial differentiation is acropetal toward the main as well as the lateral apices.

Vasculature of the inflorescence

This could be distincly followed up in a series of transsections. In the inflorescence axis there occurs a ring of 9—12 medullary bundles and many intermediate strands. Among these, two strands from the intermediate ring and three from the medullary bundles enlarge and differentiate as supply of axillary reproductive shoot which is similar to that of the leaf and the vegetative branch. These traces to the axillary reproductive shoot form a cylinder

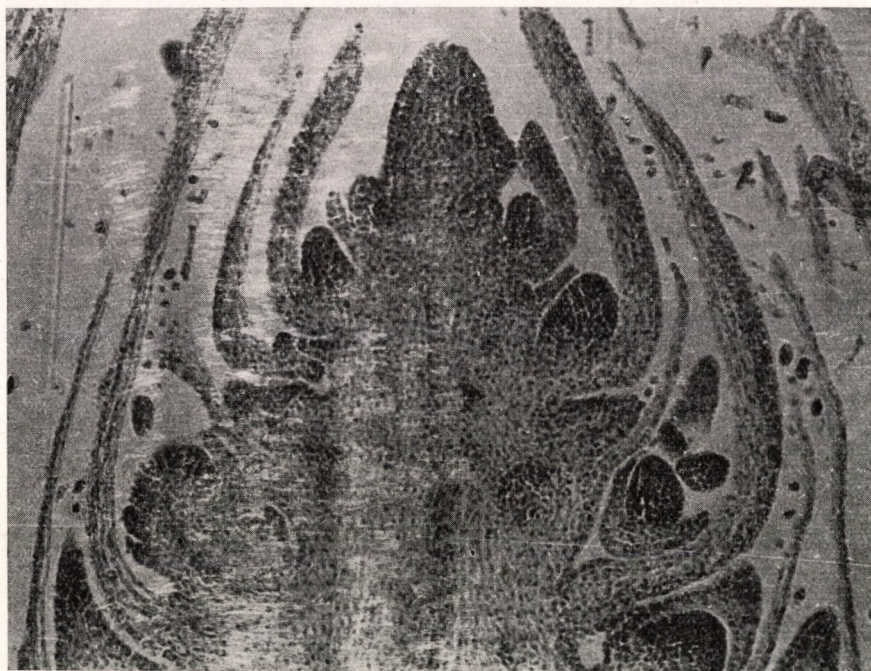



Photo 1

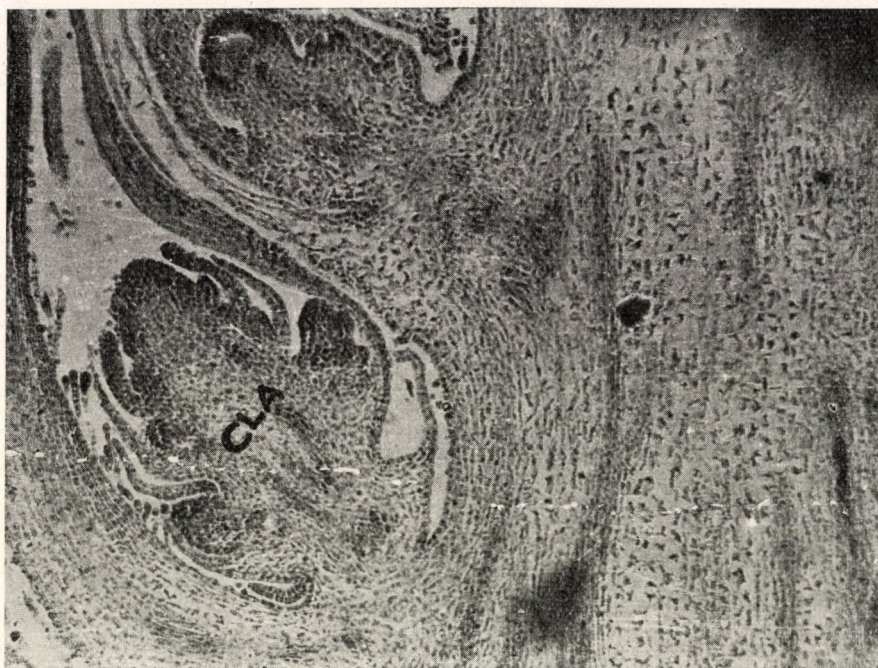
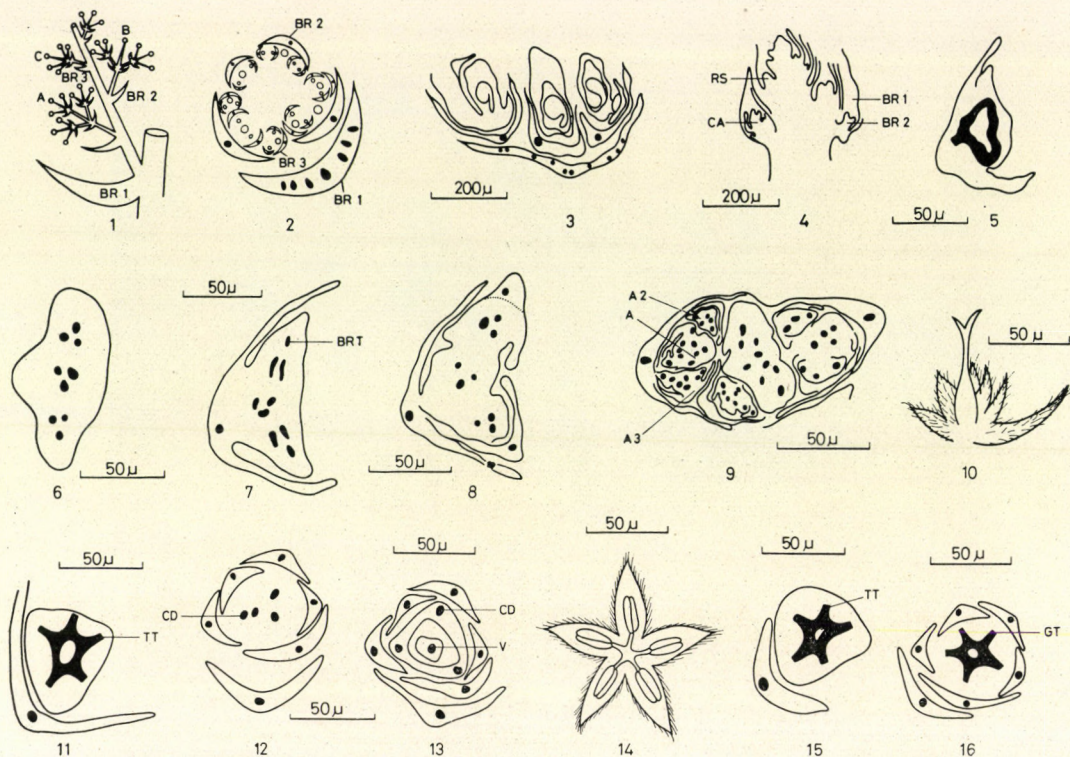



Photo 2

Figs 1–16

which breaks into nine to ten strands, nine being the most frequent number. These strands branch and give rise to intermediate bundles. The strands in the bract also may branch further so that each bract (Br. 1) comes to possess nine or more strands.

The nine bundles in a reproductive shoot form a cylinder which becomes three-lobed, each lobe containing three bundles (Figs 5, 6). The middle lobe gives out a trace to the bract which subtends the central flower (Fig. 5). These lobes further separate into three, each having bundles. Of these the lateral group gives out a trace each to its bract (bractiole according to some authors) and the remaining two bundles fuse and resolve to form three bundles (Figs 7, 8). In many cases each lateral axis may give rise to more axes in the same way as they themselves are formed (Fig. 9). The central part also may produce a cluster of three flowers (Fig. 9a).

External morphology of the female flower

The female flower has a uniseriate perianth of five tepals. The aestivation is quincuncial. The anterior tepal is larger and outer, and the posterior is smallest and inner. Of the remaing three tepals, one is outside, the second is

inside and the third with one margin inside being covered by the anterior tepal and the other outside covering the posterior tepal. The tepals are pubescent (Fig. 10).

Vascular supply of female flower

After the bract trace has separated, the three bundles fuse to form a vascular cylinder which becomes five-lobed and five traces are given out for the perianth (Fig. 11 and Microphot. 3). After the departure of the perianth

Photo 3

supply, the stele again resolves into three bundles, each giving rise to a trace which forms carpellary dorsals (Fig. 12). Further up, the three strands left in the axis fuse to form a mass in the central region which supplies the ovule (Fig. 13).

External morphology of male flower

The number and arrangement of tepals in the male flower is similar to that of the female flower, but the tepals of male flower are larger than those of female flowers. The stames, five in number, are antitepalous. The anthers are oblong and the attachment of filaments is dorsal (Fig. 14).

Vascular supply to male flower

It differs from that of the female flower in certain features. The perianth supply is given put in the same way but the stele does not get resolved into three strands after this supply departs; instead, it splits into five strands and each proceed to the antitepalous stamens (Figs 15, 16).

Discussion

BAKSHI and CHHAJLANI (1954) discussed the nature of the inflorescence in *Amaranthaceae* at length. According to these authors the original form of the inflorescence appears to have been a raceme of dichasia in which the axis of each dichasium ends in a flower and subsequent growth continues through a bud in the axil of each bracteole. They have stated that the reduction process continued resulting in a condition observed in *Pupalia lappacea* where each dichasium has one fertile flower surrounded by the remains of the others. Further reduction and transformation of the arms of the dichasium into scales has resulted in a condition seen in *Digera arvensis*. Ultimately a stage is reached where the scala also disappeared. This stage is observed in *Psilostachys sericea* (BAKSHI, 1952), *Pupalisa lappacea*, *Achryanthus apera* and *Gromphrena globosa* (BAKSHI and CHHAJLANI, 1954).

To this series of reduction it would be interesting to add *Amaranthus leucocarpus*. Here also the inflorescence has a raceme of dichasia in which the axis of the dichasium ends in a flower and further growth continues by means of buds in the axilis of bracteoles. The cymose cluster, developing from a cluster apex, bears a maximum of nine flowers composed of three dichasia. From this there is a regular reductional series; by further reduction of lateral members (only one each) a stage with five flowers is attained; with further reduction two surviving lateral members of lateral dichasia disappear leading to a cluster with three flowers. This reduced cluster of three flowers does not represent a single dichasium but three dichasia representing the central flower of each dichasium. As a result of the condensation of the axis, these three flowers appear to belong to the same dichasium.

RAO (1963) has indicated an interesting parallelism between *Proteaceae* and *Amaranthaceae*. According to him the single flower in *Amaranthaceae* represents a surviving member of the lateral branch system, just like the flower pair in *Proteaceae*. In *Amaranthus leucocarpus* the surviving member is the central flower of the dichasium and three such flowers in a reduced cluster are the three central members of three dichasia. RAO (1963) further adds that the flower in *Amaranthaceae* represents the results of phylogenetic fusion of the primordia of an ancestral flower pair such as that of *Proteaceae*. Developmental study of the inflorescence in *Amaranthus leucocarpus* does not give

any such indication. *Psilostachya sericea* (BAKSHI, 1952) and *Amaranthus aspera* (BAKSHI and CHHAJLANI, 1954) show three traced vascular supplies to tepals. In *Digera arvensis*, JOSHI and RAO (1934) reported univeined tepals in a few flowers, while BAKSHI and CHHAJLANI (1954) observed univeined uppermost perianth leaves and three veined lowermost perianth leaves. In *Amaranthus leucocarpus* tepals and stamens receive one trace each and the gynoecium has three dorsals and a ventral one (formed by the fusion of three strands). It appears therefore that *Digera* indicates a transitional stage in reduction of tepal supply, and *Amaranthus leucocarpus* shows further reduction.

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ZEITGEMÄSSE TAXONOMIE DER FESTUCA OVINA-GRUPPE

Von

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(Eingegangen am 20. Mai 1972)

The study furnishes a modern critical elaboration of the taxa in the *Festuca ovina* species-group occurring in Hungary. The following species, subspecies and their infraspecifico units are discussed: *F. ovina* agg.: *F. ovina* s. str., *F. tenuifolia*, *F. cinerea* agg., where belong in the field *F. pallens*, *F. vaginata* agg.: *F. vaginata*, × *F. stricta* (*pallens* × *rupicola*), *F.* × *wagneri* (in all probability *vaginata* × *rupicola*), *F. valesiaca* agg.: *F. dalmatica*, *F. pseudodalmatica*, *F. valesiaca*, *F. rupicola* ("*F. sulcata*"), *F. pseudovina.*

The first chapter contains the following cytotaxonomic data: *F. ovina* 14 (published 28—70), *F. tenuifolia* 14, *F. pallens*: 14!, 28!, 42!, *F. vaginata*: 14!, *F. stricta*: ?, *F. wagneri*: 28 !, *F. dalmatica* 28!, *F. pseudodalmatica*: 28!, *F. valesiaca*: 14!, 28!, 42!, *F. rupicola* 14, 28, 42!, *F. pseudovina*: 14!, 28 !. (The ! sign indicates checked domestic data.)

The second part is a key to the species and forms of higher order, the third part is the survey of all taxa that can be discussed in the *F. ovina* group. A new combination is *F. arenicola* (Prod.) Soó.

The additional notes and the critical remarks in the supplement refer to the works of Beldie and Horánszky et al. (1972).

The author contends that the species of the *F. ovina* group can be systematized only in anatomically and biometrically, the cytotaxonomic data failed to provide safe results so far; they are to be completed by accurate caryo-type analyses (as in some French, Czechoslovakian and Polish papers). Modern cytogenetic examinations are necessary in the case of species with doubtful origin. Biometric population analyses are also useful.

1. Zytotaxonomische Informationen

Die Taxa der Hackelschen Kollektivart *Festuca ovina* (eher Artengruppe mit mehreren Aggregaten) sind nur auf anatomischem-biometrischem Weg zu bestimmen. So verfuhren Monographen der Gattung bzw. der Artengruppe seit Hackel (1878, 1882) bis zu den modernen Bearbeitern (vgl. die Literatur, bes. Soó 1955, Simon 1963, Schwarzová 1967, Horánszky 1970). Eine Unterscheidung auf zytotaxonomischem Weg ist eben an den am meisten kritischen Kleinarten kaum möglich, da diese — nur die sicheren Angaben berücksichtigt — mehrere Karyotypen besitzen. Ganz abgesehen von den als *F. ovina* s. latiss. mitgeteilten Chromosomenzahlen (cf. Löve et Löve 1961 p. 40:14, 28, 42, 56, 70, Fedorow et al. 1969 p. 530: 14—70, incl. Bidault 1964: 14, 28, 56)* besitzen wir eben aus Ungarn Data von *F.*-Arten, deren

* Die Zahlen 21 und 35 beziehen sich bestimmt auf hybridogene Taxa. Das Buch von Fedorow bzw. Bolkhowskih und Mitarbeitern ist mit Vorsicht zu gebrauchen; die unter

Exemplare (gesammelt von PÓLYA und FELFÖLDY) von mir anatomisch und biometrisch revidiert wurden (vgl. Soó 1963), doch sind auch die Mitteilungen von BAKSAY ganz zuverlässig.

Festuca ovina agg. **F. ovina** L. s. str. keine Angabe aus Ungarn, aus der Slowakei (LIPTÁKOVÁ 1963) 14. Wohl besitzt aber die Kleinart auch tetraploide und hexaploide, evtl. oktoploide und dekaploide Rassen (vgl. die mitgeteilten Chromosomenzahlen).

F. tenuifolia Sibth. (*F. capillata* Lam.). Nur fremde Angaben, alle 14, die Kleinart ist diploid. Die der *F. ovina* L. s. str. nahestehende zirkumpolare *F. supina* Schur hat aber diploide (14) und tetraploide (28) Karyotypen, letztere eben aus der Hohen Tatra nachgewiesen (HADAČ et HASKOVÁ 1956), vgl. LÖVE et LÖVE 61. Die noch dieser Gruppe zugerechnete nordische *F. vivipara* (L.) Smith is wohl tetraploid (28), doch wurden auch die Zahlen 21, 42, 49 (FLOVIK 1939, fehlen in LÖVE et LÖVE) angegeben.

F. cinerea agg. **F. cinerea** Vill. 1785 und *F. glauca* Lam. 1788 gehören wohl zum Formenkreis derselben Art (STOHR), die westeuropäisch-submediterran und in Mitteleuropa bis nach Mitteldeutschland und der Schweiz verbreitet ist und ebenfalls diploid: 14 (LITARDIÈRE 1923, BIDAULT 1963) und tetraploid: 28 sein kann (GAGNIEU et BRAUN 1961, BIDAULT 1963), wie die südösteuropäische Kleinart, also auch unsere Pflanze:

F. pallens Host, die auch 2n: 14 und 28 besitzt, wie das BAKSAY 1956: 331 (Bükkgebirge 14, Naszály, Budaer Berge, Vértes 28) bestimmt hat. FELFÖLDY (ex Soó 1958: 199, 1963: 430) sammelte auf der Tihanyer Halbinsel auch hexaploide *F. pallens*! Die Karyotypen unterscheiden sich morphologisch nach der biometrischen Untersuchung von etwa 60 Exemplaren in nichts (Soó 1958), ähnlich sind aber auch die Pflanzen des Balatongebietes. Alle drei Rassen wurden auch von STOHR (in ROTHMALER 1963: 42) aus Deutschland erwähnt, der sonst 2n: 42 und 70 auch für *F. cinerea* angibt. Es ist ein Irrtum von LÖVE, dass *F. glauca* 2n: 28, (56, BIDAULT 1966) diploid und *F. pallens* tetraploid ist. **F. pallens* ist von Frankreich und Mitteldeutschland bis zum Kaukasus verbreitet, STOHR gibt aus Siebenbürgen auch *F. cinerea* subsp. *crassifolia* (Gaud.) Stohr und var. *curvula* (Gaud.) Stohr an. Die auffallendere subsp. *pannonica* (Wulf. ex Host) Soó wurde zytologisch noch nicht untersucht, sehr wahrscheinlich ist sie polyploid.** *F. pallens* hat also in Ungarn 3 Karyotypen: 14, 28, 42.

Synonym-Namen veröffentlichten Originaldaten kommen meist mehrfach vor z. B. *F. altissima* und *sylvatica*, *F. elatior* und *pratensis*, *F. capillata* und *tenuifolia*, usw. oder sogar unter mehreren Gattungsnamen, wie die *Dactylorhiza*-Arten als *Orchis*, *Dactylorchis* und *Dactylorhiza*.

* Nach BIDAULT hat sie diploide (»subvar. *exilior*«), tetraploide (»subvar. *euglauca*«) und hexaploide (»subvar. *macrophylla*«) Rassen.

** Nachträgliche Anmerkung: BELDIE (1972: 533 ff.) zählt subsp. *crassifolia* und »subsp.« *curvula* von mehreren Fundorten aus Rumänien auf, ebenso zog er »subsp.« *arenicola* (Prodan) aus der Dobrudscha zu *F. cinerea* agg.

F. vaginata W. et K. eine eigene Art, bisher nur diploid: 14 bekannt [PÓLYA 1949, Acta Geobot. Hung. 6: 127, 135 (fig.), s. auch unten] BAKSAY 1956 l. c., ferner SCHWARZOVÁ 1967: 404, u. zw. für var. *vaginata*, var. *margittaii* (var. *incrassata*) und »subsp. *mucronata*« (var. *amethystina*), für dieses Taxon ist der älteste und gültige Unterartname subsp. *dominii* (Kraj.) Soó 1955. Verwandte Arten sind *F. psammophila* Hackel ex ČELAK., 2n: 14 (SCHWARZOVÁ); *F. caesia* Smith 1808 (*F. polesica* Zapal. 1904, vgl. Soó 1955, STOHR 1959, 1963) 2n: 14 (LÖVE 1944, die Angabe von BRANDBERG, ebenfalls 2n: 14 in Ark. Bot. B. No. 3, 1948, bezieht sich auf *F. vaginata*, da seine Testpflanze aus Debrecen stammt; *F. beckeri* Hackel 1882, 2n: 28. Über diese Kleinarten vgl. Soó 1955: 196—198. Vielleicht gehört zu meinem *F. vaginata* agg. auch noch die umstrittene »*F. pallens* ssp. *arenicola* Prodan Bul. Acad. Agronom. Cluj 5: 193 (1935) incl. ssp. *mamaiae* l. c. 195«, mit spitzen Deckspelzen (gluma inferior) und ± rauhen Blättern, d. h. *F. arenicola* Soó comb. n.*

F. × stricta Host. wohl *pallens* × *rupicola*, schon früher (vgl. Soó 1955: 199) als hybridogene Art betrachtet. 2n unbekannt, die Angabe 42 bei LÖVE ist falsch, FELFÖLDY hat sie nie mitgeteilt. Die zytotaxonomisch-zytogenetische Untersuchung ist deshalb erwünscht.

F. × wagneri Degen, Thaisz et Flatt 1905 emend. Soó 1963, wohl aus der Kreuzung *vaginata* (14) und *rupicola* entstanden (Soó 1955: 199 als *F. stricta* var. *hungarica*, Májovský 1963 als *F. javorkae*, Soó 1963 als *F. wagneri*); die beiden Arten kommen oft zusammen vor, *F. wagneri* var. *hungarica* bildet in *Astragalo-Festucetum rupicolae* eine Subass. [*F. strictae* Pócs, *F. wagneri* Kovács—Láng, letztere nähert sich der *F. vaginatae* (2n: 28 LACZA Ann. Mus. Nat. Hung. 52 (1960); 183 als *F. stricta*, auch Baksay in LÖVE 1961, p. 42 als *F. conflicta*].

F. valesiaca agg. Dazu zähle ich in Ungarn folgende Arten:

F. dalmatica (Hackel) Richter, in Ungarn (Villányer Gebirge) als var. *pannonica* Simon, 2n: 28 (SIMON 1963 p. 148, Fig.!).**

F. pseudodalmatica Krajina ex Domin. Diese Art steht zwischen *F. dalmatica* (der sie im Aufbau des Stengels und der Epidermis näher steht) und *F. valesiaca* (oft im Habitus und mit den schmalen Blättern); sie wurde von mir früher zur letzteren, später zur *F. dalmatica* als Unterart gezogen, sie ist aber eine selbständige Kleinart. (NYÁRÁDY 1964 zog sie als var. zu *F. valesiaca*, BUIA 1972 als var. zu *F. dalmatica*, vgl. dagegen die Arbeit von SIMON) 2n : 28, BAKSAY 1957: 173, FELFÖLDY ex Soó 1963, SIMON l. c. Fig.! der Karyotyp

* BELDIE zitiert von derselben Stelle (Jud. Galaţi: Hanu Conachi) *F. vaginata* »ssp. *buiae*« (d. h. var. *incrassata* Krajina) und *F. cinerea* ssp. *arenicola*, was zeigt, dass es sich hier um die Gruppe *F. vaginata* handelt. (Nachträgliche Anmerkung.)

** BIDAULT veröffentlicht für seine »*F. ovina* subsp. *sulcata* var. *eudalmatica*« die Nummern n: 24 und 25, 2n: 49, ich bezweifle aber, dass er die echte *F. dalmatica* untersucht hat. Sonst sind seine Mikrophotos der Karyotypen sehr gut.

scheint ein anderer zu sein als jener von *F. dalmatica.*) Mit *F. cinerea* agg. hat die Art nichts zu tun.

F. valesiaca Schleich. ex Gaud. Aus Ungarn haben wir zwei Zahlen 2n: 14 (Tornaer Karst, auch Slowakei) nach BAKSAY 1958: 125, u. zw. für die var. *tenuis* und 2n: 28 (Tihany) nach FELFÖLDY 1947: 13, 1951: 182, var. *valesiaca* cf. SOÓ 1963: 430. Wahrscheinlich besitzt aber auch diese Art 3 Karyotypen (2n: 14 auch bei LITARDIÈRE 1923, BRANDBERG 1948, BIDAULT 1966), denn GAGNIEU et BRAUN 1959 haben auch 2n: 42, also eine haploide Rasse mitgeteilt. Ebenso gibt BIDAULT 1967 für die var. *angustiflora* 2n: 42 an.

F. rupicola Heuff. [*F. sulcata* (Hack.) Nym.] Es wurden diploide (14) — so BRANDBERG 1948, PETROVA 1965 —, tetraploide (28) — so STÄHLIN 1929, PETROVA 1965 — und hexaploide (42) Rassen — so eben aus Ungarn (FELFÖLDY 1947: 13, 1951: 182, PÓLYA 1949: 127) aber auch von anderen: LEVITSKY und KUZMINA 1927 (ex LÖVE), BRANDBERG 1948 und PETROVA 1965 mitgeteilt, weitere zytotaxonomische Untersuchungen sind noch nötig.

F. pseudovina Hack. ex Wiesb. Beide Karyotypen wurden auch aus Ungarn gemeldet, so 2n: 14 nach PÓLYA 1948: 147 Fig., var. *salina*!), FELFÖLDY 1951: 182 und 2n: 28 (FELFÖLDY 1947: 13 Fig., 1957: 102—3 Fig., ex SOÓ 1963: 430, var. *pseudovina*!). Die diploide Rasse wurde noch von BRANDBERG 1948, die tetraploide noch von SOKOLOWSKAJA und STRELKOWA 1940, 1948 publiziert. Die 2n:35-Kreuzung von Tihany (FELFÖLDY 1951 l.c. ist wahrscheinlich *F. valesiaca* × *rupicola*, leider ohne Beschreibung (von mir nicht gesehen), dann entspricht sie der zweifelhaften *F. meredisensis*, s. am Ende des Schlüssels.

An den hybridogenen Arten, aber auch an anderen, die eine Zwischenstellung zeigen (z. B. *F. pseudodalmatica*), sind zytogenetische Untersuchungen nötig, aber auch so eingehende Analysen der Idiogramme wie sie z. B. ČINČURA an *F. pseudodalmatica* durchgeführt hat. Ebenso wichtig ist aber eine ausführliche biometrische Bearbeitung, auch mit statistischen Methoden, und Varianzanalyse (wie HORÁNSZKY neuerdings betont hat) einzelner homogener Populationen, bes. der verschiedenen zytotaxonomischen Rassen jener Arten, die mehrere Karyotypen besitzen, wie *F. pallens*, *F. valesiaca*, *F. rupicola*, *F. pseudovina*, vielleicht diese mit schon bekannten morphologisch-systematischen Taxa identifizieren. Während der Untersuchung der grundlegenden histologischen Merkmale darf man nicht vergessen, dass sich diese im Laufe der Ontogenie der Blätter (weniger unter dem Einfluss der Umwelt) ändern; zur Bestimmung ist ein Querschnitt des unteren Drittels des voll entwickelten Blattes nötig (vgl. BORSOS 1957).*

* Zwei Fehler bei HORÁNSZKY, 1969: Von der Gattung *Festuca* haben wir eine neuere fast vollständige Monographie (SAINT-YVES: Tentamen. Claves analyticae Festucarum Veteris Orbis. Revue Bretonne 1927, mit späteren Ergänzungen (bis 1934, vgl. SOÓ Acta Bot. Hung. 2n: 210). SIMON (1964) hat eben biometrisch-statistisch nachgewiesen, dass *F. pseudodalmatica* k e i n e Unterart von *F. dalmatica* ist, wie ich sie früher nannte.

2. Bestimmungschlüssel der Taxa der *F.-ovina* Gruppe im pannonischen Raum

1a Lamina foliorum basalium etiam sicca cylindrica vel latere utroque convexa, strato sclerenchymatoso subepidermali confluenti, continuo (rariter inaequali, interrupto)

b Lamina foliorum basalium saltem sicca compressa, latera utroque longitudinaliter sulcata, fasciculis sclerenchymatosis subepidermalibus 3 (—5) non continuis, lamina vulgo aspera, palea inferior seu glumella normaliter aristata 7

2a Lamina folii capillaris vel setacea, 0,3—0,6 mm crassa, apicem versus ± aspera 3

b Lamina foliorum 0,6—1,3 mm crassa 4

3a Lamina folii 0,3—0,6 (—0,8) mm lata, glumella 2,2—4,5 mm crassa, aristata, folia 5—7 nervia **F. ovina** L. s. str.

var. *ovina*: Folia 0,3—0,6 mm crassa, spicula 4—5,8 mm longa, planta viridis, glabra, glumella glabra vel (subvar. *hispidula*) dorso pilosa, margine barbata, rarius (subvar. *subglaucescens*) planta ± glauca

var. *firmula*: Folia 0,5—0,8 mm crassa, 7-nervia, glumella glabra vel (subvar. *lemanii*) pilosa, planta viridis, rarius (subvar. *glaucostachya*) spiculae pruinosae, variegatae

var. *pseudogenuina*: uti var. *ovina*, sed spicula 5—8,5 mm longa, planta viridis, glabra vel scabra, glumella glabra vel (subvar. *deylii*) pilosa resp. ciliata, rariter (subvar. *sillingeri*) planta ± glauca

var. *pilifera*: uti var. *pseudogenuina*, sed folia, vaginae, caulis sub paniculam et spiculae hirsutae

b Lamina folii 0,3—0,45 mm crassa, glumella 1,5—2,5 mm longa, mutica vel paullo aristata, folia plerumque 5-nervia, panicula angusta **F. tenuifolia** Sibth.

4a Stratum sclerenchymatosum subepidermale continuum, aequaliter crassum. Folia juncea, glauco-pruinosa, laevia (rarissime scabrida) 5

b Stratum sclerenchymatosum subepidermale ± interruptum, inaequale Folia viridia (rarius glaucescentia cf. *F. valesiacam*), ± scabra 6

5a Gluma superior acuta. Glumella 4—5,5 mm longa, aristata, arista 0,5—2 mm longa **F. pallens** Host

var. *pallens*: Planta 15—30 cm alta, folia 7—9-nervia, 0,7—1 mm crassa, spiculae 4—6 (8)-florae, 4,5—9 mm longae, planta glauca, raro (f. *stenoglauca*) viridis, glumella glabra vel parce pilosa resp. ciliata (f. *barbata*) vel villosa (f. *hirsuta*)

var. *scabrifolia*: uti var. *pallens*, sed folia scabra, glumella hirsuta vel glabra (f. *degenii*)

var. *umbrosa*: Planta 30—60 cm alta, folia cauli saepe longiora, spiculae 6—8 florae, 8—10 mm longae, planta glauca, raro (f. *virens*) viridis

subsp. *pannonica*: Planta 30—60 cm alta, folia 11—13-nervia, 0,9—1,3 mm crassa, spiculae 5—9-florae, 6—10 mm longae, panicula scaberrima, glumella glabra, rarius (f. *borhidiana*) parce pilosa vel ciliata

b Gluma superior mutica. Glumella 3—4,5 (5) mm longa, saepius non aristata **F. vaginata** W. et K.

var. *vaginata*: Folia 0,55—1 mm crassa, 7—11-nervia, spiculae 3—7-florae, 4—8 mm longae, glumella mutica, glabra, vel parce pilosa resp. ciliata (f. *ciliolata*) vel villosa (f. *plusiostachya*)

var. *amethystina*: uti var. *vaginata*, sed glumella aristata, arista 0,2—0,8 (1) mm longa vel (subvar. *mucronata*) tantum mucroniformi, —0,2 mm longa

var. *incrassata*: Folia 0,9—1,35 mm crassa, 11—15-nervia, spiculae 4—8-florae, 6—10 mm longae, glumella 4—5 mm longa, mutica vel (f. *valida*) breviter aristata (0,2—0,5 mm)

6a Folia plerumque 7-nervia, 0,7—1 mm crassa, stratum sclerenchymatosum epidermale inaequaliter crassum vel in 5—7 fasciculos divisum, Panicula 8—15 cm longa, spiculae 4—6-florae, 6—8 cm longae.

F. wagneri Degen, Thaisz et Flatt

in Hungaria tantum var. *hungarica*, spiculae glabrae vel (f. *horanszkyana*) ± pilosae, arista 0,8—2,5 mm longa

b Folia 5—7-nervia, 0,6—0,9 mm crassa, stratum sclerench. simile, panicula 3,5—7,5 cm longa, spiculae uti praecedentis, arista 1—3,5 mm longa, glumella scabra vel (f. *braunii*) ± pilosa. **F. stricta** Host

7a Folia plerumque fasciculis sclerenchymatosis 5 8

b Folia plerumque fasciculis sclerenchymatosis 3 (si 5 adsunt, tunc spicula 7,5 mm-o brevior) 9

8a Folia crassa (0,6—0,9 mm), rigida, vaginae basalium breves, crassae, panicula angusta, 6—8 (—10) cm, spicula 8—9,5 mm, glumellae 4—4,5 mm, arista —3 mm longa in var. nostra *pannonica*

F. dalmatica (Hack.) Richt.

b Folia tenuia (0,4—0,7 mm), flexuosa, vaginae basalium longiores graciles, panicula 8—15 cm longa, lata, spicula 7—10 mm, glumella (4) 4,5—5,5 mm, arista 1—1,35 mm longa* **F. pseudodalmatica** Krajina

9a Spicula 4,5—5,5 (—6) mm, glumella 2,8—3,5, arista 1—1,5 (—2) mm longa. Folia 0,35—0,6 mm crassa, planta 10—30 (40) cm alta

F. pseudovina Hackel ex Wiesb.

var. *pseudovina*: Planta 20—30 (40) cm alta, viridis vel rarius ± pruinosa, folia plerumque arcuato-flexuosa, panicula angusta, 3—7 cm longa, glumella glabra, raro (f. *hirtiflora*) breviter pilosa

var. *salina*: Planta —10 (—15) cm alta, saepe rutila, folia rigida,

* Data in SIMON 1964 et SOÓ—KÁRPÁTI 1968 non exacta.

saepe setacea, panicula ovata, 2—3 cm longa, glumella glabra, raro ciliata (f. *barbulata*)

b Spicula 6—8 cm, glumella 3,5—5,5 mm longa. Folia 0,35—0,8 mm crassa, planta vulgo 30—70 cm alta 10

10a Folia 0,35—0,6 mm crassa, fasciculis sclerenchymatosis 3 (rarissime 5). Spicula (5) 5,5—7 (—9) mm, glumella 3,5—4,8 mm, arista 1—3 (—3,5) mm longa, plerumque glabra **F. valesiaca** Schleich.

var. *valesiaca*: Planta pruinosa, spiculae glaucescentes, glumella glabra vel rarissime (f. *velebitica*) dorso pilosa

var. *tenuis*: Planta viridis, spiculae canovirides, rarissime villosae (f. *villosa*), glumella glabra vel (f. *krajinae*) ciliata. Huc: subvar. *angustiflora* spicula subulato-lanceolata, 3,5—4,3 mm longa, glabra, arista 1—2 mm

b Folia 0,6—0,8 mm crassa, 3 fasciculis sclerenchymatosis firmis. Spicula (5) 6—7,5 (raro 8—12) mm, glumella (3,5—) 4,5—5,5 (6) mm, arista (0,5—) 1—3 mm longa, glumella saepius hirta

F. rupicola Heuff. (*F. sulcata* (Hackel) Nym.)

In territorio nostro tantum var. *rupicola*: glumellae dorso breviter pilosae vel tantum ciliatae resp. (f. *hirsuta*) tota superficie pilosa—villosa vel (f. *sulcata*) glabra. Folia glabra, laevia, rarius (f. *hispida*) cum vaginis et glumellis pilosa—villosa. Planta viridis, rarissime (f. *glaucantha*) pruinosa. Formae intermediae (hybridogenae?) *F. valesiaca*—*F. rupicola* habent folia tenuia (0,3—0,6 mm crassa) spiculas 6—8 mm, glumellas 4,5—5,5 mm longas (*F. meredisensis* Nyár.) .

3. Übersicht der Arten und infraspezifischen Taxa der *F. ovina*-Gruppe*

F. ovina agg. sensu nostro (*F. ovina* L. s. l.)
Syn.: *F. ovina* subsp. *euovina* Hack. 1882, A. et G. 1901

I. **F. ovina** L. Spec. pl. ed. 1. 73 (1753) s. str. et auct. recent. (seit Nym. 1882).
Syn.: subsp. *vulgaris* Čelak. 1867, Hegi 1908, var. *vulgaris* Koch 1837, Hack. 1882, *F. vulgaris* Hay. 1918, *F. euovina* Dom. 1935
var. *ovina* (syn.: *genuina* Gren et Godr. 1859, *euvulgaris* Litard. 1923)
subvar. *ovina* (*euvulgaris* St.-Yves 1913, *genuina* Kozl. 1925) f. *ovina* (*viridiflora* Kraj. 1930). Dazu: f. *variegata* Kraj. 1930, f. *breviculmis* Kraj. 1930, f. *longiaristata* Kraj. 1930 (arista 1,3—2,2 mm), f. *supiniformis* Nyár. 1964, f. *brevifolia* Nyár. 1964, f. *laevifolia* (Hack. 1882) Kraj. 1930 (folia et vaginae laeves, tantum sub apice scabrae), f. *capillifolia* Kraj. 1930 (folia filiformia, 0,25—0,4 mm crassa), f. *tatrensis* Kraj. 1930, *breviaristata* Kraj. 1930 (incl. sf. *viridis* et *violascens* Kraj. 1930), f. *vivipara* Baumg. 1816
subvar. *hispidula* Hack. Mon. Fest. 87, 1882, Litard. 1923 p. f. (? *villosa* Baumg. 1816)
subvar. *subglaucescens* Hack. ex Rohl. Sitzb. Böhm. Ges. Wiss. 1911: 8 emend. Soó incl. f. *arenosa* Kraj. 1930

* Die im Bestimmungsschlüssel nicht erwähnten Formen sind von geringem systematischem Wert, einige sogar wohl nur Ökomorphosen. Sie werden hier namentlich aber nur ausnahmsweise mit Diagnosen aufgezählt; diese findet man in den zitierten Werken von HACKEL, KRAJINA, NYÁRÁDY usw., auch in meiner Synopsis florae vegetationisque Hungariae V 1973.

var. *firmula* (Hack. Mon. Fest. 87, 1882 p. subvar.) Hegi Ill. Fl. Mitt. eur. I: 331 (1908)
subvar. *firmula* (*typica* Kraj. 1930), huc: f. *firmula* (*vulgaris* Kraj. 1930), f. *submucronata* Soó 1971 (*breviaristata* Kraj. 1930 non var. *genuina* f. *breviaristata* Kraj.) — arista 0,1—0,5 mm —, f. *aculeolata* Soó 1971 (*longiaristata* Kraj. 1930 non var. *genuina* f. *longiaristata* Kraj.) — arista 2—2,5 mm —
subvar. *lemanii* (Bast. Ess. Fl.-Maine et Loire 36, 1809 p. sp.) Hack. l. c. 1882 p. f. (Kraj. 1930: 189 p. subvar.)
Dazu: f. *lemanii* (*eu-lemanii* Kraj. 1930, *hirtella* Podp. 1926), f. *multiflora* Kraj. 1930, f. *flaccida* Kraj. 1930
subvar. *glaucostachya* Rohl. l. c. (1901)
var. *pseudogenuina* Kraj. Acta Bot. Boh. **9**, 188 (1930)
subvar. *pseudogenuina* (*typica* Kraj. 1930) f. *pseudogenuina* (*communis* Kraj. 1930), f. *glabra* Kraj. 1930, f. *supinoides* Kraj. 1930, f. *umbrosa* Hack. 1882, f. *polyantha* Kraj. 1930
subvar. *deylii* Kraj. l. c. (1930) (*hispidula* Hack. 1882 p. p.) Huc: f. *ciliolata* Kraj. 1930, f. *sciaphila* (Schur 1866 p. sp.) Hack. 1882
subvar. *sillingeri* Kraj. l. c. (1930), Markgr.-Dbg. ex Janchen 1963 p. var.
subvar. *pilifera* St.-Yves Bull. Soc. Bot. Fr. **71**, 29 (1924), Markgr.-Dbg. l. c. p. var. (*suzana* Podp. 1926)
Weitere, meist aus dem Westen bekannte Varietäten:
var. *turfosa* Markgr.-Dbg. 1950 p. subvar., var. *rohlenae* Kraj. 1930 p. subvar., var. *guestphalica* (Boenningh. ex Rchb. 1830 p. sp.) Hack. 1882 p. subvar., Hegi 1908 p. var., var. *firmulacea* Markgr.-Dbg. (1938 sub *F. trachyphylla*) 1950 p. subvar., Stohr 1960 p. var. Die var. *heteropachys* St.-Yves 1924 wurde neulich von Patzke 1965 als einige Kleinart betrachtet.

2. **F. tenuifolia** Sibth. Fl. Oxon. 44 (1794)
Syn.: *F. capillata* Lam. 1778 nom. illeg., *F. ovina* var. *mutica* Retz. 1795, var. *tenuifolia* M. et K. 1823, Čelak. 1867 p. subsp., var. *paludosa* Steud. 1821, var. *capillata* Hack. 1881, Arc. 1894 p. subsp.
Formae: f. *tenuifolia* (*typica* Junge 1913), f. *frisia* (A. et G. 1901 sub *F. ovina*) Soó 1971, f. *arenaria* (Junge 1913 sub. *F. ovina*) Soó 1971

F. cinerea agg. (*F. cinerea* Vill. 1785 emend. Stohr 1960, Rauschert 1960, *F. duriuscula* L. 1753 emend. Kraj. 1930, nom. dubium, *F. glauca* Lam. 1788 emend. Hyl. 1945, auch bei Soó 1955)

In der pannonischen Florenprovinz nur:
3. **F. pallens** Host Gram. Austr. 2: 63 (1802)
Syn.: *F. cinerea* Vill. subsp. *pallens* Stohr 1960, Rauschert 1960, *F. glauca* Lam. subsp. *pallens* O. Schwarz 1949, Richt. 1890 p. var., var. *major* Hagenb. 1831, *F. ovina* L. var. *glauca* subvar. *pallens* Hack. 1882, subsp. *glauca* var. *pallens* Kozl. 1925 p. var., *F. duriuscula* L. var. *longifolia* Kraj. 1930 (sed non *F. longifolia* Thuill. 1790) et var. *pallens* Kraj. 1930. p. p., *F. cinerea* var. *curvula* Stohr 1960 p. p. non *F. curvula* Gaud. 1811, *F. nitida* Kit. 1863, *F. glauca* auct. hung.
var. *pallens* (*duriuscula* var. *pallens* Kraj. 1930) f. *pallens* (subvar. *typica* Kraj. 1930) — f. *stenoglauca* Borb. Balaton fl. 318 (1900), Soó 1955 sub *F. glauca*, 1964 sub *F. cinerea* (*F. duriuscula* auct. hung., *F. intermedia* auct. an R. et Sch. 1817, *F. csikhegyensis* Simk. 1906) — f. *barbata* (Hack. Termr. Füz. 2: 284, 1878 sub *F. glauca*) Soó Acta Bot. Hung. **17**, 116 (1971). Syn.: *F. ovina* subvar. *pallens* f. *puberula* Hack. 1882, Zapał. 1906, Soó 1955 sub *F. glauca*, Stohr 1960 sub *F. cinerea*, *pallens* var. *subpuberula* Borb. 1900 — f. *hirsuta* (Heuff. Verh. ZBG **8**, 196, 1858 sub *F. glauca*) Soó l. c. 1971 (*cinerea villosa* auct. vix Schrad. 1806 sub *F. ovina*, var. *curvula* f. *villosa* Stohr 1960 p. p.)
Weitere Formen: f. *scabens* (Beck 1890 sub f. *glauca*) Soó 1971 (*rigidifolia* Borb. 1887 non 1879), f. *longearistata* (Naumann ex Rauschert 1960 sub *F. cinerea*) Soó 1971 — arista 2—3 mm —, f. *polonica* Soó 1971 — arista 3,5—4,5 mm —, f. *elongata* (Hack. 1878 sub *F. glauca*) Soó 1971 [*stenostachya* (Hack. 1882 sub *F. ovina*) Nyár. 1964], f. *curvula* (Hack. l. c.) Nyár. 1964, vix *F. curvula* Gaud. 1811, f. *depauperata* (Hack. l. c.) Zapał. 1906, f. *minoriflora* Borb. 1887, f. *rachsturmensis* (Kraj. 1930 sub *F. duriuscula* subvar. *slovenica*) Soó 1971, f. *fatrensis* (Kraj. l. c.) Soó 1971, f. *pseudorepens* Borb. 1887
var. *scabrifolia* (Hack. ex Rohl. Sitzb. Böhm. Ges. Wiss. 1899, 24: 3 sub *F. glauca*) Markgr.-Dbg. ex Janchen Catal. Fl. Austr. 1. Erg. 109 (1963) — f. *degenii* (St.-Yves Ann. Conserv. Jard. Bot. Genève **17**: 80, 1913 p. subvar. *F. ovinae* var. *glaucae*) Soó l. c. 1971

var. *umbrosa* (Heuff. l. c. 1858 sub *F. glauca*) Soó l. c. 1971 (*longifolia* Kraj. 1930 sub *F. duriuscula*, an etiam Hack. 1878 sub *F. glauca*, Soó 1955 sub *F. glauca*, 1964 sub *F. cinerea*) Huc: f. *umbrosa* (*longifolia typica* Kraj. 1930) — f. *virens* (Kraj. l. c. 194 p. subvar *F. duriusc.* var. *longifoliae*) Soó l. c. 1971. Weitere Form: f. *pubiculmis* (Hack. ex Rohlena l. c. 4, 1899 sub *F. duriuscula*) Soó 1971 (*hirticaulis* Soó 1964, non *F. cinerea* var. *pubiculmis* Stohr)

subsp. **pannonica** (Wulf. ex Host Gram. Austr. IV. tab. 62, 1809 p. sp.) Soó comb. n., Jáv. 1924 comb. incerta, Borb. 1900 p. var. (*F. ovina* var. *pannonica* Koch 1837, *F. duriuscula* var. *pannonica* Kraj. 1930, *F. glauca* var. *pannonica* Soó 1955, *F. cinerea* var. *pannonica* Rauschert 1960, Soó 1963) Huc: f. *borhidiana* (Soó Acta Bot. Hung. **2:** 194 sub *F. glauca*) Soó l. c. 1971.

Weitere Varietäten: var. *rigurosa* (Schur 1866 p. sp.) Soó 1971 aus Siebenbürgen (BELDIE vereinigt sie zu Unrecht mit dem Typ, nachträgliche Bemerkung)

var. *sandomiriensis* (Zapał. 1906 sub *F. duriuscula*) Soó 1971 aus Galizien

F. vaginata agg. (S. oben). In pannonischem Raum nur

4. **F. vaginata** W. et K. ex Willd. Enum. Horti Berol. 116 (1809)

Syn.: *F. ovina* var. *vaginata* Hack. 1883, Hegi 1908 p. subsp., var. *amethystina* Koch 1837 — s. unten —, *F. caesia* Sm. subsp. *vaginata* Patzke 1961, *F. pallens* var. *vaginata* Borb. 1900, *F. arenaria* Kit. ex Steud. 1821, *F. distans*, *F. obtusa* Kit. ex Hack. 1878 et Jáv. 1929

var. *vaginata* (var. *subjuncea* Kraj. 1930, *F. ovina* var. *amethystina* subvar. *vaginata* Litard. 1945, *F. amethystina* Host var. *mutica* Hack. 1878) Formae: f. *vaginata*, — f. *ciliolata* Deg. Magy. Bot. Lap. 22: 63), — f. *plusiostachya* (Borb. Balaton fl. 318, 1900 sub *F. pallente*. Soó Acta Bot. Hung. 2: 190, 1955; ferner f. *semiglauca* Borb. 1886, f. *buiae* (Prod. p. subsp. *F. glaucae*) Nyár. 1964 (*F. pallens* subsp. *buiae* Prod. 1957, var. *careii* Prod. 1957),* f. *vivipara* Borb. 1886 (*prolifera* Borb. 1900 sub *F. pallente*)

var. *incrassata* Kraj. l. c. 200 (*F. dominii* var. *margittaii* Kraj. l. c., *F. vaginata* var. *margittaii* Soó in Soó et Jáv. 1951, Schwarzová 1967); dazu f. *valida* (Kraj. l. c. sub *F. dominii* Soó 1955 l. c.)

var. *amethystina* (Koch Syn. Fl. Germ. ed. 1. 812, 1837 p. var. *F. ovinae*) Soó 1964 in Ad honorem Prof. Soó, p. 10 (*F. dominii* Kraj. 1930 var. *genuina* Kraj. 1930, *F. vaginata* subsp. *dominii* Soó 1951, 1955 p. var., *F. ovina* var. *amethystina* subvar. *dominii* Litard. 1945)

subvar. *amethystina*

subvar. *mucronata* (Hack. l. c. 97. 1882 sub *F. ovina* var. *vaginata*) Soó comb. n., Soó 1905 p. f., Schwarzová 1968 p. subsp. (*F. amethystina* Host. var. *subaristata* Schur 1866, *F. pallens* var. *subaristata* Borb. 1900, *F. dominii* subvar. *mucronata* Kraj. 1930) Huc: f. *urziceniensis* Nyár. 1964

Hybridogene Arten:

5. **F. stricta** Host Gram. Austr. **2**:61, tab. 86 (1802)

Syn.: *F. ovina* ssp. *sulcata* var. *stricta* Hack. 1882, subvar. *stricta* Markgr-Dbg. 1950, *F. valesiaca* Schleich. subsp. *stricta* Hegi 1908, *F. sulcata* var. *stricta* Nym. 1890, *F. duriuscula* var. *stricta* Schur 1866, *F. angulata* Kit. ex Hack. 1878

var. *stricta* f. *stricta* — f. *braunii* Soó l. c. 1971

Weitere zweifelhafte Var.: var. *polita* (Hack. in Halácsy) Soó 1955 Balkan

6. **F. wagneri** Degen, Thaisz et Flatt Magy. Bot. Lap. **4**: 30—31 (1905) emend. Soó 1963

Syn.: *F. sulcata* subsp. *wagneri* Jáv. 1924 comb. incerta, *F. ovina* subsp. *sulcata* var. *wagneri* St.-Yves 1928, *F. conflicta* Baksay ex Löve 1961 nom. nud.

var. *wagneri* (*F. sulcata* subvar. *wagneri* Degen etc. l. c., aber auch binär!, *F. javorkae* Májovský var. *wagneri* Májovský Acta fac. rer. nat. univ. Comenianae, Botanica **9**: 326, 1963), huc: f. *slovaca* (Májovský) Soó 1963

var. *hungarica* (Soó Acta Bot. Hung. **9**, 199, 1955 p. var. *F. strictae*) Soó Acta Bot. Hung. **9,** 431 (1963) (*F. javorkae* var. *javorkae* Májovský l. c.), — f. *horánszkyana* (Soó 1955 l. c. p. f. *F. strictae*) Soó 1963 l. c.

F. valesiaca agg. sensu nostro

7. **F. dalmatica** (Hack. Mon. Fest. 102, 1883 p. var. *F. ovinae* subsp. *sulcatae*) Richt. Pl. Eur. I 95 (1890)

* Weiteres Syn.: *F. vaginata* subsp. *buiae* Beldie 1972 incl. var. *dubia* Beldie 1972, nachträglicher Zusatz.

Syn.: *F. vallesiaca* pr. *dalmatica* A. et G. 1900, *F. sulcata* var. *grossiflora* Nyár. 1964
var. *dalmatica* cum formis f. *pseudorupicola* Thaisz 1902, f. *breviglumis* Nyár. 1964, f. *subdalmatica* Nyár. 1964
var. *pannonica* Simon Ann. Univ. Budapest Sect. Biol. **7:** 144 (1964) (var. *circumsepta* Nyár. 1964 neigt zu *F. pallens*, vielleicht hybridogen?)

8. **F. pseudodalmatica** Krajina ex Domin Acta Bot. Boh. **8:** 61 (1929)
Syn.: *F. dalmatica* subsp. *pseudod.* Soó 1958, var. *pseudod.* Beldie 1972, *F. valesiaca* subsp. *pseudod.* Soó 1943, var. *pseudod.* Soó ex Nyár. 1941, Nyár. 1964.
Formen: f. *pseudodalmatica* (*virescens* Dom. 1929), f. *glaucovirens* Dom. 1929, f. *angulosa* (Nyár. 1964 sub *F. valesiaca*) Soó 1971

9. **F. valesiaca** Schleicher ex Gaudin Agrostol. Helv. I: 242 (1811)
Syn.: *F. ovina* var. *valesiaca* Link 1833, Koch 1837, ssp. *vallesiaca* pr. *euvallesiaca* A. et G. 1900, subsp. *sulcata* var. *valesiaca* Hack. 1882, *F. vallesiaca* subsp. *euvallesiaca* Hegi 1935, *F. ovina* subsp. *valesiaca* Kozl. 1925, etc.? *F. duriuscula* var. *umbrosa* Heuff 1858
var. *valesiaca*, f. *valesiaca* (*genuina* Kraj. 1930, *tenuis* Nyár. 1964 non Hack.), f. *velebitica* Degen et Lengyel Fl. Veleb. I: 543 (1937) (? var. *lasiantha* Schur 1866, incl. f. *subhirta* Nyár. 1964)
Weitere Formen (z. T. sehr unbedeutend, so die von Nyár. 1964): f. *banatica* Deg. 1915 — arista 2,5 – 3,5 mm —, f. *halanensis* Deg. 1937 (*hirta* Nyár. 1964) f. *longifolia* Ravaruț ex Nyár. 1964, f. *longispiculata*, f. *minutiflora*, f. *strictiflora*, f. *hirtiformis*, f. *subtriflora*, f. *hirtiformis*, f. *subtriflora*, f. *flabelliformis*, f. *tricostata*, f. *doljensis* Nyár. 1964
var. *tenuis* (Hack. Termr. Füz. 2: 288, 1878 p. subsp. *F. duriusculae*) Kraj. l. c. 210 (1930) (*F. ovina* var. *pseudovina* subvar. *tenuissima* Hack. l. c. 103, var. *valesiaca* subvar. *tenuissima* St.-Yves 1924, *F. valesiaca* var. *pseudovalesiaca* (Błocki) Zapał. 1906)
subvar. *tenuis* f. *tenuis*, *f. krajinae* Soó Acta Bot. Hung. **17:** 116, 1971 (*tenuis* Kraj. 1930 non Hack.), f. *villosa* (Prod. Bul. Acad. Agron. **5:** 25 (1934) Soó l. c. 1971 (*F. pseudovina* var. *villosa* Prod. 1934)
subvar. *angustiflora* (Hack. Mon. Fest. 102, 1882 p. subvar. *F. ovinae* var. *pseudovinae*) Kraj. l. c. 208 (1930)
Syn.: *F. ovina* subsp. *valesiaca* var. *pseudovina* f. *angustiflora* A. et G. 1900, var. *valesiaca* subvar. *angustiflora* St.-Yves 1924, *F. pseudovina* f. *angustiflora* Jáv. 1924, huc: f. *hirtula* Nyár. 1964
Vielleicht gehören zu *F. valesiaca* var. *strictifolia* (Opiz) Kraj. 1930 und var. *podperae* Kraj. 1930, dagegen kaum f. *crassifolia* Nyár. et Şerbanesu 1964
F. valesiaca—rupicola: *F. meredisensis* (Nyár. Bul. Grad. Bot. Cluj **8:** 103 (1928) p. f. *F. valesiacae*) Nyár. Rev. Roum. Biol. Botan. **9:** 171 (1964) Syn.: *F. sulcata* f. *tenuisulcata* Nyár. 1939, var. *tenuisecta* Prod. 1939, als Formen: f. *subrupicola* (Nyár. 1964 sub *F. sulcata*) Soó 1971 und f. *bisulcata* (Nyár. et Soó ex Nyár. 1964 sub *F. sulcata*) Soó 1971

10. **F. rupicola** Heuff. Verh. ZBG **8:** 233 (1858) emend. Soó Mezőség fl. 11 (1949)
Syn.: *F. sulcata* (Hack. 1881 p. var. *F. ovinae*) Nyman 1882, Oborny 1882, *F. ovina* subsp. *sulcata* Hack. 1881, var. *genuina* Hack. 1882, subsp. *vallesiaca* pr. *sulcata* A. et G. 1900, *F. vallesiaca* subsp. *sulcata* Hegi 1908, *F. duriuscula* subsp. *typica* Hack. 1878, *F. hirsuta* Host 1802 emend. Soó 1951 (nom. illegit.), *F. ovina* var. *pannonica* Griseb 1844, *F. stricta* Host subsp. *sulcata* Patzke 1961, *F. anceps* Kit. 1863, *F. compressa* Kit. 1863, *F. multiflora* Kit. ex Hack. 1878, *F. tokayana* Kit. ex Hack. 1878, *F. subulata* Kit. ex Jáv. 1929
subsp. *rupicola* var. *rupicola* (*F. ovina* subsp. *sulcata* var. *genuina* Hack. 1882, subsp. *vallesiaca* pr. *sulcata* var. *typica* A. et G. 1900, var. *sulcata* St.-Yves 1924, Stohr 1955, *F. ciliaris* Kit. ex Hack. 1878)
f. *rupicola* (*eurupicola* Soó 1949, *F. ovina* ssp. *sulcata* subvar. *barbulata* Hack. 1882, f. *dasyantha* St.-Yves 1924, f. *barbata* Stohr 1960, *F. vallesiaca* subsp. *rupicola* Simk. 1887, Hegi 1908 p. subvar., *F. sulcata* var. *rupicola* Beck (1870), Jáv. 1924 p. f., var. *barbulata* Richt. 1890, *F. duriuscula* f. *barbata* Hack. ex Wiesb. 1880, *F. hirsuta* var. *rupicola* Borb. 1887) cum sf. *ciliata* (Podp. 1922 sub *F. sulcata*) Soó 1971 spicula tantum margine ciliata
— f. *hirsuta* (Host 1802 Gram. Austr. **2,** 61, tab. 85, 1802 p. sp.) Soó Mezőség fl. 11, 1949, RAUSCHERT 1960 (*F. ovina* subsp. *sulcata* subvar. *hirsuta* Hack. 1882, Stohr 1960 p. f., var. *hirsuta* Link 1833, *F. vallesiaca* subsp. *hirsuta* Simk. 1887, Hegi 1908

p. subvar., *F. sulcata* var. *hirsuta* Richt. 1890; Jáv. 1924 p. f., subvar. *glabrifolia* Kraj. 1930, *F. duriuscula* var. *subhirsuta* Schur 1866, f. *hirsuta* Wiesb. 1880). Huc sf. *hirtiflora* Nyár. 1964

— f. *hispida* (Hack. 1882 Mon. Fest. 105 p. subvar. *F. ovinae* subsp. *sulcatae*) Rauschert Feddes Repert. **63:** 274, 1960, Soó 1968 (*F. valesiaca* var. *hispida* Hegi 1908, Stohr 1960 p. f., *F. duriuscula* var. *hirsuta* Schur 1866, *F. sulcata* var. *hispida* Richt. 1890, Jáv. 1924 p. f., *F. hirsuta* var. *hispida* Soó 1951)

— f. *sulcata* (Hack. l.) Soó 1949 l. c., Rauschert 1960 (*F. ovina* subsp. *sulcata* subvar. *typica* Hack. 1882, ? *F. duriuscula* var. *elata* Schur 1887, *F. vallesiaca* subsp. *sulcata* var. *typica* Hegi 1908, *F. sulcata* var. typica Zapał. 1906, *F. hirsuta* var. *sulcata* Borb. 1887)

— f. *glaucantha* (Hack. l. c. 1882 p. subvar. *F. ovinae* subsp. *sulcatae*) Rauschert 1960, huc sf. *glaucantha-hirsuta* (Weighart ex Podp. 1926 sub *F. sulcata*) Soó 1971 Weitere Formen (bzw. sf.) mit kahlen Ährchen: f. *pauciflora* (Heuff. l. c. 196, 1858 sub *F. duriuscula*) Soó 1971, Nyár. 1941, 1964 sub *F. sulcata*, *strictiflora* (Nyár. 1941 sub *F. sulcata*) Soó 1971, f. *longifolia* (Nyár. et Prodan 1939 sub *F. sulcata*) Soó 1971, f. *incurvata* (Nyár. 1942 sub *F. sulcata*) Soó 1971, f. *tricostata* (Nyár. 1964 sub *F. sulcata*) Soó 1971, f. *pseudobulbosa* (Nyár. et Soó 1943 sub *F. sulcata*) Soó 1971, Nyár. 1964 sub *F. pseudovina*, f. *prorepens* (Rohl. 1923 sub *F. sulcata*) Soó 1971, f. *inaequata* (Kit. ex Hack. 1878, sub *F. sulcata*, Jáv. 1924) Soó 1971, ferner mit behaarten Ährchen f. *hackelii* (Zapał. 1906 sub *F. sulcata*) Soó 1971

Weitere Varietäten: var, *sulcatiformis* (Markgr.-Dbg. 1950) Markgr.-Dbg. ex Janchen 1963 (Österreich, Deutschland), var. *coziae* (Nyár. 1964 sub *F. sulcata*) Soó 1971 (Südkarpaten), var. *saxatilis* (Schur 1866 p. sp.) Soó 1971 bzw. eher subsp. *saxatilis* (Schur) Rauschert 1960 mit vielen Formen (Siebenbürgen); mir unbekannt ist die subsp. *pachyphylla* (Deg. ex Nyár. ap. Csürös Contrib. Bot. Univ. Cluj, 1962: 46 p. sp.) Beldie 1972 p. 555. *F. sulcata* var. *grossiflora* Nyár. 1964 gehört zu *F. dalmatica*, *F. craiovensis* Buia et Nyár. 1964 zu *F. valesiaca* (Soó 1971: 117, Beldie 1972)

11. **F. pseudovina** Hack. ex Wiesbaur Öst. Bot. Zeitschr. **30:** 126 (1880) non Rydberg 1900
Syn.: *F. ovina* subsp. *sulcata* var. *pseudovina* Hack. 1882, var. *valesiaca* subvar. *pseudovina* St.-Yves 1924, A. et G. p. pr., *F. duriuscula* subsp. *parviflora* Hack. 1878, *F. valesiaca* subsp. *pseudovina* Simk. 1887, Stohr 1955 p. var., var. *parviflora* Hegi 1908, . *F. pulchra* Schur 1866 sec. Simk. 1887, *F. compressa* Kit. 1863, *F. racemosa* Kit. 1863, *F. angulata*, *F. aristata* Kit. ex Hack. 1878

var. *pseudovina* (subvar. *typica* Hack. 1882, var. *parviflora* (Hack. l. c.) A. et G. 1900) f. *pseudovina* (*hackelii* Kraj. 1930) — f. *hirtiflora* Borb. Magyar homokp. 70 (1886)

Weitere Formen: f. *subpruinosa* Borb. 1887, f. *pruinosa* Kraj. 1930, f. *subseptemflora* Nyár. 1964 (*F. racemosa* Kit. ex Hack. 1878), f. *longiaristata* Nyár. 1964 — arista 2 mm —, f. *urzicenii* Prod. 1957, f. *parva* A. et E. I. Nyár. 1964

var. *salina* (Kern. ex Hack. Mon. Fest. 103, 1882 p. sp.) Hack. l. c. p. subvar., Soó comb. n. f. *salina* — f. *barbulata* Nyár. l. c. 172, 1964, ferner f. *rutila* (Hack. 1901 p. subvar.)

Nachtrag (15. V. 1972)

Mein Manuskript über die *F.-ovina*-Gruppe aufgrund meiner Bearbeitung in der Synopsis florae vegetationisque . . . Hungariae, Bd. V. (abgeschlossen Apr. 1971, erschien Febr. 1973) war schon fertig, als ich drei weitere Mitteilungen über *Festuca* im April-Mai 1972 erhielt. Die wichtigste unter ihnen ist die Bearbeitung der Gattung von A. Beldie in der Flora R. P. R., Bd. XII., die — obwohl sie die beste Arbeit über *Festuca* in rumänischer Sprache ist und viele Irrtümer von Prodan und A. et E. I. Nyárády korrigiert hat —, für mich nicht viel Neues enthält, da ich mehrere Verbesserungen schon in der Synopsis bzw. in Acta Bot. Hung. 1971 durchgeführt habe. Einige Angaben nach Beldie habe ich in der vorliegenden Arbeit in Form nachträglicher Bemer-

kungen noch berücksichtigt. Wir gebrauchen einen engeren Artbegriff als BELDIE oder die neueren deutschen Autoren (wie RAUSCHERT, STOHR usw.), von den französischen (wie BIDAULT, LITARDIÈRE, ST.-YVES) ganz zu schweigen.

Eben jetzt ist eine provisorische kurze Publikation von HORÁNSZKY, JANKÓ und VIDA erschienen. In ihr sind die neu angefangenen zytogenetischen Untersuchungen am wärmsten zu begrüssen, um so weniger die sog. »Arbeitshypothese« — wohl von HORÁNSZKY —, die einerseits die bisher bekannten zytotaxonomischen Angaben z. T. unberücksichtigt liess, z. B. die hexaploide *F. pallens*!, die diploide *F. rupicola*, die tetraploide *F. pseudovina*! usw., andererseits ganz unwahrscheinliche Abstammungen vermutet, wie *F. wagneri* von *vaginata* und *pseudovina* (statt *rupicola*), *F. pseudodalmatica* aus *pseudovina*, *valesiaca* und *pallens*, usw. Gründliche zytogenetische Versuche werden hier das letzte Wort zu sprechen haben. Nomenklatorisch: warum die überholten Namen nach SOÓ—JÁVORKA 1951 gebrauchen? In SOÓ—KÁRPÁTI 1968 sind schon die richtigen da, so statt *F. glauca F. pallens*, statt *F. sulcata F. rupicola*. Sonst werden nicht einmal die neuesten *Festuca*-Bearbeitungen erwähnt (vgl. mein Literaturverzeichnis!).

Über die synökologisch-soziologische Rolle der *F. ovine*-Kleinarten, vgl. die Angaben in meiner Synopsis, für *F. valesiaca* mangelhaft, da die meisten ungarischen Zönologen oft »*sulcata-valesiaca*« angeben, obwohl die beiden Kleinarten ein anderes synökologisches Verhalten besitzen, wie darauf kürzlich in einer sorgfältigen Arbeit HROUDOVÁ-PUČELIKOVÁ hingewiesen hat.

Auch in der bulgarischen Literatur herrscht über die *F. ovina* Gruppe ein grosses Durcheinander. Die Bearbeitung von ACHTAROV (Bull. Inst. Bot. Acad. Bulg. Sofia **3**: 53—74: 1953) ist ganz überholt. In meinen *Festuca* Studien (1955) habe ich die Arten *F. vaginata* von Gebedze (Beloslaw) »Dikili-Tas« unweit von Varna (mit den Formen *amethystina* = *dominii* und *mucronata*) — wo sie die charakteristische Sandsteppengesellschaft *Festucetum vaginatae bulgaricum* bzw. *Festuca vaginata-Lepidotrichum üchtritzianum* Ass. bildet (SOÓ 1953, 208) und *F. callieri* (Hack.) Markg. aus einer *Asphodeline taurica-Onosma taurica* Ass. (l. c. 202—203) mitgeteilt. Dass ich, der Bearbeiter der ungarischen Sandpflanzengesellschaften (Acta Bot. Hung. 1957) und monographischer Bearbeiter der *F. ovina* Gruppe diese Arten besser kenne, als die bulgarischen Kollegen, ist evident. Ausserdem aus den biometrischen Angaben der bulgarischen (l. c. 193) und der ungarischen Pflanze (l. c. 190) und der anatomischen Struktur (l. c. 212) von *F. vaginata* ist unzweifelhaft, dass es sich um gleiches Taxon handelt. Allein VALEV hat in der Flora RP Bulg. 1: 395 diese Gruppe richtig behandelt, seine *F. duriuscula* nebst Varietäten gehören wohl zu *F. pallens*. Umsomehr unbegründet ist in der neuen Ausgabe der Flora Bulgarica von STOJANOV—STEFANOV—KITANOV (p. 127) »ssp. *ovina* var. *duriuscula* (*F. vaginata* Soó non W. K.)« — *F. duriuscula* ist bekanntlich ein nomen dubium — und noch mehr von GANTSCHEV (1968: 102 108), dass

die Pflanze von Beloslav »*F. pallens* var. *psammophylla* (sic!) Hack« ist. Herr GENTSCHEV weiss es nicht, dass *F. psammophila* einerseits nicht zu *F. pallens* gehört, anderseits eine nord-mitteleuropäische Kleinart ist (cf. Soó l. c. 197), die jedenfalls der *F. vaginata* nahe steht. Die Pflanze des Golo-Brdo und Lülin ist die echte balkanisch-osteuropäisch-mittelasiatische Art *F. callieri*, aus der Krim beschrieben, die bulgarische (lebend untersuchte) und krimische *F. callieri* (Original!) sind sowohl aufgrund der äusseren und inneren Morphologie (Soó l. c. 212 Fig. 15—16) und der Struktur der Blattepidermis (HORÁNSZKY bei Soó l. c. Taf. 4—5!) dieselben. Dazu als Syn.: *F. pseudovina* f. *mrkvickana* Acht. 1953 fig. 6! früher *F. ovina* ssp. *dalmatica* var. *mrkwickana* (Acht.) Stof. 1948, *F. pallens* ssp. *transitoria* Nyár. f. *mrkvickana* Gan. 1968: 107. *F. callieri* ist sowohl von *F. pseudovina* (Stojanov etc. 127 Syn.), wie von *F. pallens* grundverschieden, sie gehört zu den Zwischenarten der *F. cinerea* agg. und *F. valesiaca* agg. (Soó Syn. Fl. Veg. Hung. V: 288). Darin hat GANTSCHEV nur Recht, dass die var. *tenuis* Hack. nicht zu *F. pseudovina*, sondern zu *F. valesiaca* zählt, letzte Art fehlt sonst in Fl. RP Bulg. 397. Merkwürdig publiziert GANTSCHEV l. c. 109 (eine Seite nachher) wieder *F. vaginata* aus Bulgarien.

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SUPPLEMENT TO SPECIES AND SUBSPECIES OF THE GENUS OPHRYS*

By

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On the basis of recent literature (especially SUNDERMANN 1970, and O. et E DANESCH 1972), and of written communication, the author has compiled supplements to his work entitled Species and Subspecies of the Genus *Ophrys*, 1970. In numerous cases he criticizes the inferences of the above authors, particularly the new taxa determined by DANESCH and his co-workers. In the survey, the Ophryses designated with numerals are agg.-s, while below them are the names of small species and of the transituses.

Since the publication of the concise summary containing the identification key of the European species, the description of the species and subspecies, and the enumeration of the extra-European taxa of the genus *Ophrys* not only communications submitting the diagnoses of new "species" and "subspecies,, have been published but also the book "*Ophrys*-Hybriden" (pp. 268, Bern, 1972) by DANESCH, husband and wife, excellent photographers but amateurs in systematics and genetical speculations; the book contains, besides innumerable new *Ophrys* hybrids, the description of many new "species" and the elevation to specific rank of other taxa. (The submitted new combinations are, without a basionym, all invalid, the same as in SUNDERMANN's book, 1970). This latter author published a rather severe but opposite criticism about DANESCH's book (Orchidee **23**, 166—168 and 170—171, 1972).

Some supplementary remarks and corrections to the text of my work:

p. 380. **O. lutea** subsp. *Murbeckii* (Fleischm.) Soó (ssp. *minor* O. et E. Danesch 1972 nom. illeg.), subsp. *melena* also in It (South)

p. 380. *O. fusca* subsp. *iricolor* (*O. Fleischmannii* auct. sic Nelson non Hay.)

subsp. *omegaifera* (Fleischm.) Nelson (*O. Dyris* Maire! cf. p. 390) var. *omegaifera* Labellum uti subsp., obscure brunneo villosum,— var. *Fleischmannii* (Hay. Feddes Repert. **22,** 388, 1926 p. sp.) Soó comb. n. emend. (*O. Heldreichii* Fleischm. 1925 non Schlecht. 1923, *O. fusca* var. *Fleischmannii* Soó 1926) labellum non geniculato-reflexum, atroviolaceo villosum, speculum obscure griseo-violaceum, cum typo, sic Cr. Cyp. *O. omegaifera* is according to GREUTER

* Acta Bot. Acad. Sci. Hung. **16,** 373—392 (1970).

Boissiera **13,** 188—189 (1967) a "distinct monomorf species", to SUNDERMANN (1970: 63) and in my opinion a small species of *O. fusca* agg. (transitus!)

p. 382. subsp. *sicula* also in It (South); SUNDERMANN relegates this taxon, and also subsp. *sipontensis* (O. et E. Danesch 1972 p. sp. nom. illeg.) as well as subsp. *panormitana* (cf. p. 383) to the hybridogeneous form array of *O. arachnitiformis*; the latter is a *sicula* — *Spruneri* transitus!

p. 382 subsp. *Tommasinii* (Rchb. f. 1851 p. var., Vis. 1852 p. sp.) a distinct susp. eastern. Diagnosis in SCHLECHTER, Monogr. 1: 108-109, drawing Taf. 5. fig. 17. are good, in SCHULZE (1894) both very bad! the figure of the labellum by RCHB. f. is better. I have seen the original from VISIANI (San Pietro di Nembi, Herb. Mus. Wien) and others specimens from Yugoslavia and Corfu (Soó Bot. Arch. 23:132, 1927!) The figures in NELSON (T. XLVIII. 1-6) are good different from the western exemplars of the subsp. *litigiosa* (fig. 7-23). NELSON is writing „im Westen nicht oder nur ganz schwach, in der Ostmediterraneis (so auf Kreta) deutlicher gehöckert". SCHLECHTER: habe ich an den von mir untersuchten Blüten zwei kurze aber doch deutliche Höcker feststellen können. „I also. Petala (ex SCHLECHTER) „breiter, dreinervig", ex SOÓ "nonnunquam = sometimes trinervia", in subsp.*litigiosa* always "uninervia" Labellum margine glabro flavo-viridi (cf. NELSON fig. cit.), but also often in subsp. *litigiosa*. The subsp. *Tommasinii* have thus characteristic stamps and independent area: Cr(NELSON, HERMJAKOB in litt.), Ju, Gr Isles, Rhodos? (surely not *litigiosa*)

p. 382. **O. sphegodes** subsp. *garganica* Nelson l. c. 195—196/1962, O. et E. Danesch p. sp. nom. illeg. incl. subsp. *provincialis* Nelson l. c. (cf. Sundermann 67)

subsp. *sphegodes* similis, tepala externa saepius albida vel roseola, interna latiora, etiam purpureo-fusca, labellum magnum (—12 mm × —16 mm). Speculum majus, saepe labellum fere totum obtegens, striae ad basim lateraliter elongatae. It (South), Ga (South), Hs (Catalaunia), non est hybridogena sups. *sphegodes* also in Hs (Catal.) after **Bolós** 1950, (**Arnold** in litt.)

p. 383. subsp. *Aesculapii* (Renz) Soó, Stearn 1958 p. var. *good* small species. Labellum integrum, rotundum, planum, egibbosum, medio fuscum, margine lata (—3 mm) glabra. Tepala flava. Gr pluribus locis, cf. DANESCH 1969: 42, SUNDERMANN 67, HERMJAKOB in litt. *O. Aesculapii* subsp. *pseudoaraneifera* Renz l. c. 1928 (non *O. pseudoaraneifera* Murr 1898) = *O. Renzii* Soó est transitus ad subsp. *sphegodes*

subsp. *Helenae* (Renz l. c. 251, 1928 p. sp.) Soó comb. n. non est lusus (NELSON, SOÓ) sed subsp. (*O.*) *mammosae*. Flores magni. Tepala obscure viridia, Labellum integrum, egibbosum, tota superficie fusco- vel violaceo-puberulum, inconspicue maculatum. Gr (Corfu—RENZ, Epirus, Olympos — HERMJAKOB in litt.)

p. 283. subsp. *parnassica*: *O. sphaciotica* Fleischm. Öst. Bot. Zschr. **74,** 186 (1925) est transitus (*O.*) *mammosa* — *O. Spruneri*

The taxa missing from the recent works (NELSON, SUNDERMANN, DANESCH) and belonging to *O. sphegodes* s. l., are discussed on pp. 390—391, namely the Algerian subsp. *Moesziana* Soó, the Cicilian subsp. *Boissieri* Soó (transitus ad subsp. *mammosam* est subsp. *Vierhapperi* (Soó Report. **24,** 35 (1927) p. var. *O. araneif.* ssp. *parnassicae*) Soó comb. n., further the Near East-Iranian subsp. *Sintenisii* (Fleischm. et Bornm.) Nelson 1962, p. 181 (transitus ad

(*O.*) *Spuneri* est subsp. *amanensis* Nelson p. 182). This latter cannot be considered a distinct species, since the tubularly elongated connectivum occasionally appears also in the Grecian (*O.*) *mammosa* (HERMJAKOB in litt.), also SUNDERMANN (Orchidee **20,** 82, 1969; and p. 69, 1970) allocates it there under. Its taxonomic status is therefore disputed, tending, like *parnassica*, often with "labello ± trilobo" towards (*O.*) *Spruneri*, with which DANESCH groups it together.

O. caucasica Woronow is a Caucasian taxon; the datum from Amasia refers to *Vierhapperi* mentioned above, from the (*O.*) *mammosa* array; subsp. *transhyrcana* (Czern.) Soó, from Iran, Turkestan, and the Altai, is more distinct, approaching *parnassica*, being "labello trilobo, gibbis parvis".

p. 381. The hybridogeneous derivation of *O. ferrum-equinum* (Danesch: *argolica* × *Spruneri*) is hardly acceptable, though subsp. *Gottfriediana* (Renz) Nelson is already a transitus to (*O.*) *Spruneri*.

p. 384. **O. Bertolonii.** To the form array of this species belong, according to DANESCH, the hybridogeneously derived *O.* × *bertoloniiformis* (*Bertolonii* × *sphegodes*) O. et E. Danesch Orchidee **22,** 117 (1971) from South Italy (Mte Gargano) and subsp. *benacensis* Reisigl l. c. **23,** 163 (1972), described as its subspecies, with an extensive area from the Lake Como to Istria, and *O. promontorii* O. et E. Danesch l. c. **22,** 258 (1971) from the Mte Gargano (as *O. Bertolonii* × *O. sphegodes* subsp. *garganica*), surely a local race (cf. Sundermann l. c. **23,** 166—168). I do not think it precluded that in *Bertolonii* populations individuals originating by intogressive retrocrossing with *O. sphegodes* may also occur, as also in other genera. The *Bertolonii* × *sphegodes* hybrids (primary F_1 and other generations, retrocrossings and constant forms) are especially variable, and a great number of forms have been described (cf. KELLER—SOÓ 75—76; REINHARD in DANESCH 256). The several transitus between the small species of *O. sphegodes* are probably of a similar origin.

p. 385. *O. argolica* and *Reinholdii* follow 8. *O. ferrum-equinum* and, together with (*O.*) *straussii* (p. 391), build an agg. connected with transitional forms, as pointed out also by SUNDERMANN and DANESCH.

p. 385. **O. cretica.** The ssp. *naxia* and *karpathensis* cannot be regarded as even a local race (HERMJAKOB in litt.). The nearest ally, relegable to a common agg., is *O. Kotschyi* (p. 391), under this older specific name.

p. 385. The correct earlier name of *O. attica*, as a distinct species, is **O. carmeli** Fleischm. et Bornm. Ann. Nat. Mus. Wien 1923, 9, but it can also be regarded as a subspecies of *O. scolopax*, or more correctly, also as the small species of the *O. scolopax* agg.; the transition is subsp. **orientalis** (Renz Repert. 27: 205 [1930 sub *O. cornuta*] Soó comb. n.)

p. 387. **O. fuciflora** (Cr. 1769 sub *Orchide*) MOENCH Suppl. ad Meth. Plant. 1802: 311, Sw. 1800 nom. nud (*O. holosericea* Burm. f. Nova Acta Acad. Leop.-Carol. 4, app.: 237, 1770 sub *Orchide*) Greuter Boissiera **13,** 185,

1967). Specimen originale *Orchidis fuciflorae* Cr. est *Ophrys fuciflora*, cf. KELLER Ann. Hist. Nat. Mus. Nat. Hung. **36,** 114 (1944).

p. 387. subsp. *apulica* (O. et E. Danesch 1972 p. sp. nom. illeg.) is merely a more distributed form in South Italy, but like all other "subsp." described by DANESCH and mentioned also in my article; thus the new subsp. *gracilis* Büel et Danesch Orchidee **23,** 160 (1972) it hardly has a higher value than the other earlier described varieties (cf. KELLER—SOÓ 34—37), thus especially the eastern var. *maxima* Fleischm. Öst. Bot. Zschr. **74,** 188 (1925) "labello subquadrato-flabellato, speculo simplici, appendice trinervio, H-formi, floribus magnis" Gr, Cr, Karpathos, Rhodos, Anat, possibly regardable as a subsp. (Soó comb. n.), but forms with large flowers with another type of labellum occur also elsewhere in the area of *O. fuciflora* (such, e.g. is *apulica*, with the data Ge, It, Sa referable to it). The taxon subsp. **Lacaitae** (Lojacono Fl. Sic. III:40, 1908 p. sp.) Soó comb. n., considered by DANESCH (p. 36) a distinct species is the transitional form between subsp. *fuciflora* and subsp. *oxyrrhynchos*; Si, It (South).

p. 388. **O. exaltata.** According to DANESCH, it is hybridogeneous and allocated by them to the *ferrum-equinum* group, but it is a small species of the *O. fuciflora* agg., whose local race, described by the present author as subsp. *Sundermanni*, they incorrectly regard, under the name *O. biscutella*, as a distinct species (O. et E. DANESCH Orchidee **21,** 358, 1970).

p. 388. *O. arachnitiformis*. SUNDERMANN (73) terms it rather appositely hybridogeneous "Formenschwarm", relegating several *O. sphegodes* agg. forms under it. In fact, one may relegate here *O. sipontensis* (Gumprecht) O. et E. Danesch 1972 nom. illeg. from the Mte Gargano, *O. Morisii* Martelli Monocot. Sardoae 62, 1898 p. var. (CIFFERI et GIACOMINI Nomencl. Fl. Ital. 1. 157, 1950) from Sardinia, and as a fixed hybrid *O. catalaunica* O. et E. Danesch 1972:230 from Catalonia (*arachnitiformis* × *Bertolonii*; the older name of this combination is *O.* × *neo-Camusii* Godfery 1922). According to DANESCH (p. 188), *O. arachnitiformis* essentially differs from the primary *O. fuciflora* × *sphegodes* hybrid; this is *O.* × *Aschersonii* Nanteuil 1887, to which several nm. belong, cf. KELLER—SOÓ 77, REINHOLD l. c. 248. *O. Ruppertii* A. Fuchs 1917 is dubious. Recently reported *O. arachnitiformis*, also from Ju.

p. 390. **O. speculum** subsp. *regis-Ferdinandii*, also in Chios (HERMJAKOB in litt.).

In the followings I propose to attempt a subdividing, by the use of the recently ever more extensive term "aggregatum" (the former spec. coll.), of this extraordinarily varying, easily crossing genus, in the full flower of its evolution and rich in hybrids and transitional forms. The origin of some disputed taxa can be decided only by cytogenetical and recombinational investigations. These aggregates correspond to the few trally "good" *O.* species as recently suggested by SUNDERMANN. (The number of species in Soó (1929)

in 30, in NELSON 21, or together with the small species termed subspecies, 46, although several taxa of a higher rank are missing; in Soó (1970) 25, discounting the two dubious eastern species (*phrygia* Fleischm. et Bornm. and *Schulzei* Bornm. et Fleischm.*), in SUNDERMANN 31, in DANESCH 44.)

O. puritensis Guittonneau Bul. Soc. Bot. France **109,** 264 (1963) from Algeria is, on the basis of the description, possibly an *apifera* × *scolopax* hybrid.

O. adonidis A. Camus et Gembault from Liban is for me unknown. (Not. syst. **14,** 104, 1951 in Index Kewensis false citatum, are missing also in NELSON, SUNDERMANN, DANESCH.)

A survey, according to my system (Soó 1970:375), of the *Ophrys* aggregates, small species and transitus forms (as interpreted by the late Prof. Z. KÁRPÁTI Borbásia Nova **25,** 1—20 (1944), Ann. Biol. Debrecen, **1,** 189--198 (1950).

1. **O. insectifera** L.
2. **O. speculum** Link
3. **O. lutea** (Gouan.) Cav. cum 3 subsp.
4. **O. fusca** agg.
   - *O. fusca* Link cum subsp. *iricolor*
   - *O. omegaifera* Fleischm., magis subsp. *O. fuscae,* sine area specifica, transit in *O. fuscam*!
   - *O. atlantica* Munby cum subsp. *Hayekii*
   - *O. pallida* Rafin.
5. **O. sphegodes** vel *sphecodes* agg.
   - *O. sphegodes* Mill. cum subsp. pluribus (*sicula, garganica* etc.)
   - *O. Aesculapii* Renz resp. *O. sphegodes* subsp. *Aesculapii*
   - *O. Tommasinii* Vis. 1852 (nomen veterius) cum subsp. *litigiosa* (Camus Journ. Botan. **10,** 1—3, 1896 p. sp.) Soó comb. n.
   - *O. atrata* Lindl.
   - *O. mammosa* Desf. Huc subsp. *taurica, Helenae, Boissieri* (Soó Repert. **26,** 279 sub *O. arenifera*), *caucasica* (Woronow in Grossheim Fl. Kavk. I: 261, 1928 p. sp.) Soó comb. n.
   - *O. Spruneri* Nym.
   - ?*O. transhyrcana* Czern.
   - *Transiti* (p. p. hybridogenea)
   - *sphegodes* × *litigiosa*: *Jeanpertii* Camus

* In the first quarter of the century, the Viennese FLEISCHMANN was the best specialist of the genus *Ophrys*; I have worked up his orchidological legacy: the excellent flower analyses (there were no colour transparencies at that time!) allowed the description of several new taxa. I am quite confident that the forms distinguished by him are valid.

sphegodes × *Aesculapii*: *Renzii* Soó
sphegodes × *atrata*: *Todaroana* Macch.
sphegodes—*mammosa*: *macedonica* Fleischm. ex Soó 1927 (*pseudomammosa* Renz 1928)
atrata × *Tommasinii*: *Mansfeldiana* Soó
atrata × *litigiosa*: *Cortesii* A. Camus
mammosa × *Spruneri*: *sphaciotica* Fleischm. 1925 p. sp. (*parnassica* Vierh. 1919 p. forma) incl. *O. pseudospruneri* Soó
mammosa subsp. *Boissieri* × *Spruneri*: *Vierhapperi* (Soó 1927 cf. supra)
sphegodes subsp. *sicula* × *Spruneri*: *panormitana* (Tod. Orch. Sic. 75, 1842 p. var. *Arachn. fucifl.*) Soó comb. n.
O. × *arachnitiformis* Gren et Philippe incl. *sipontensis*, *catalaunica*, *Morisii* etc. cf. supra

6. **O. ferrum-equinum** agg.
   O. ferrum-equinum Desf. cum subsp. *Gottfriediana*
   O. argolica Fleischm. cum subsp. *elegans*
   O. Reinholdii Spruner cum subsp. *Straussii*
7. **O. Bertolonii** Moretti incl. × *bertoloniiformis*, *benacensis*, × *promonotorii*
8. **O. lunulata** Parl.
9. **O. Kotschyi** agg.
   O. Kotschyi Fleischm. et Soó 1926
   O. cretica (Vierh.) Nelson 1962
10. **O. scolopax** agg.
   O. scolopax Cav. cum 4 subsp.
   O. carmeli Fleischm. et Bornm. (*attica*) cum subsp. *orientalis*
11. **O. fuciflora** agg.
   O. fuciflora (Cr.) Moench cum pluribus subsp. (*candida*, *maxima*, *apulica* etc.)
   O. oxyrrhynchos Todaro
   tr. fuciflora—*oxyrrhynchos*: *Lacaitae* Lojac.
   O. exaltata Ten. cum subsp. *Sundermannii* ("*biscutella*")
   O. Bornmuelleri Schulze
12. **O. tenthredinifera** Willd. cum subsp. *neglecta*
13. **O. apifera** Huds. cum subsp. *jurana*
14. **O. bombyliflora** Link

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THE INFLUENCE OF SPORE NUMBER PER SURFACE UNIT ON THE COURSE OF GERMINATION IN SOME ASPERGILLUS SPECIES ON SOLID MEDIUM (PRELIMINARY COMMUNICATION)

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The effect of different conidium densities of *Aspergillus flavus*, *A. nidulans* and *A. niger* on the time variations in germination percentage was examined on Czapek—Dox agar. The results suggest that in large inocula, contrary to the small ones, a germination inducing effect prevails in the case of the three *Aspergillus* species. Assumably, the germination inducing substances accumulating in the medium are responsible for the phenomenon.

Introduction

Numerous examples are known in the literature about the fact that the time course of germination, or the final germination percentage, in "fungus spores" (conidia, asco- and basidiospores, etc.) depends, among other things, also on how many spores were placed in the unit volume of the liquid medium, or implanted in the unit surface on the solid culture medium. In part of the cases the large, while in other cases the small, inocula germinate better, according to whether the spores stimulate or inhibit the germination of one another. In the followings the formation of invariably the primary hypha is ment under germination although this word is sometimes given a different interpretation in the same work (for example, Sussmann and Halvorson, 1966).

According to the literature, it is a frequent phenomenon that by using a large inoculum the germination of the spores is relatively inhibited, in comparison with the behaviour of the small inoculum (Cochrane 1958; Sussmann 1965; Sussmann and Halvorson 1966; Lingappa and Lingappa 1965, 1966, etc.). The literature in English calls self-inhibition the germination-inhibiting effect exerted by the various spores of a species on one another.

The concrete cause of self-inhibition must be fairly variegated. It is imaginable, though to my knowledge it has not been verified in any of the cases, that the inoculated large number of spores suddenly reduces the concentration of some limiting component in the nutrient medium. Since, however, there are numerous data on the fact that the most diverse spores may contain and secrete substances inhibiting their own germination (Sussmann 1965,

SUSSMANN and HALVORSON 1966) the simplest hypothesis is to explain self-inhibition by the presence of these substances. According to LINGAPPA and LINGAPPA (1966), the extent of self-inhibition in *Glomerella cingulata* decreases if the conidium inocula are washed through distilled water. They warrant that the cause of the efficiency of this treatment is indeed the disappearance of the inhibitory substances and not traces of elements possibly taken up from the distilled water.

The inhibitory substances, primarily considered responsible for inhibition, may be various from a chemical point of view (as far as they are known in this respect). The inhibitor of *Glomerella* spores is presumably an alkaloid (LINGAPPA et al. 1967). The uredospores of certain rusts contain volatile and non-volatile inhibitors as well (SUSSMANN 1965). In the inhibited germination of large inocula of *Microsporum gypseum*, anorganic phosphate also plays a role (PAGE and STOCK 1971).

The literature describes also some cases where the relatively large inoculum does not inhibit but stimulates germination, again in comparison with the behaviour of the small inocula. SUSSMANN and HALVORSON (1966) mention such cases primarily in slime fungi (*Myxomycetes*). From the study by ROBINSON et al. (1968) it can be inferred that this phenomenon must exist in *Rhizopus* and *Mucor* species as well, for it has been stated that some species of these genera produce germination stimulating substances at the early stage of their germination, on both the liquid and the solid nutrient media. The endogenous germination stimulating substances of fungus spores are known only in a few cases chemically (SUSSMANN and HALVORSON 1966, SUSSMANN 1965). According to the latter source, there may concurrently exist stimulating and inhibiting substances in the same spore.

Although a number of publications discuss the germination of *Aspergillus* species (SUSSMANN and HALVORSON 1966, BURNETT 1968, CAMPBELL 1971) I found no data on the course of germination depending on the size of the inoculum. The studies by MEYRATH (1963), and MEYRATH and McINTOSH (1965) also only touch this problem. They study the influence of the spore inoculum size, placed in the liquid medium, on the development of *Aspergillus oryzae*. However, they do not examine the germination of the conidia directly. That is why we considered it essential to investigate the germination kinetics of the conidia of some *Aspergillus* species on solid nutrient medium depending on the size of the inoculum.

Material and method

Organisms. The wilde strains of *Aspergillus flavus*, *A. nidulans* and *A. niger* were used in the experiments.

Nutrient medium. In all experiments the CZAPEK—DOX-type solid medium was used in the following mixture: 50.0 g glucose; 2.0 g $NaNO_3$, 1.0 g KH_2PO_4, 0.5 g KCl, 0.5 g

$MgSO_4 \cdot 7H_2O$, 0.01 g $FeSO_4$, 20 g agar, 1000 ml distilled water. The pH of the nutrient medium was set to 6.5; it was autoclaved at 121°C for 15 minutes.

Preparation of the spore suspension, inoculation. 5 ml of 0.1% Tween-80 was added to 5-day old *Aspergillus* cultures on CZAPEK—DOX agar slopes. For the suspension of the conidia, the cultures were vibrated on a table shaker for 30 minutes. The conidium suspension was poured into sterile test tubes. The conidia were precipitated by slightly centrifugating them, then the supernatant was poured off and subsequently we washed with 10 ml of distilled water. After centrifugation, the washing was repeated. Then the suspension was again centrifugated and the conidia suspended in sterile distilled water. To break up the conidium chains, the suspension was again vibrated for 30 minutes. The spore density was determined in a BÜRKER chamber, and the spore number set to the values 1×10^6 and 1×10^7 conidia/ml. 10 ml of nutrient agar was poured in each of the PETRI dishes (internal diameter 9.5 cm), thus the thickness of the nutrient medium was about 1 mm, ensuring good study conditions for the microscope. In order to have the small and the large inocula exposed to the same CO_2 concentration, inoculation was carried out with small inocula (1×10^6 conidia/ml) at three points, and with large inocula (1×10^7 conidia/ml) also at three points in each of the Petri dishes. Inoculation was carried out with a suspension of one loopful quantity, which on the average equals 0.39 microlitre of liquid. The diameter of the inoculated area was about 3 mm. This procedure resulted in a relatively even conidium density; the average conidium density in small inocula was 55 conidia/mm^2, while in the large inocula 550 conidia/mm^2. After inoculation, the Petri dishes were left open in a steril box until the evaporation of the distilled water (about half an hour).

Cultivation was carried out at 37°C. To assure saturated atmosphere, filter paper soaked with sterile distilled water was placed into each of the Petri dishes.

Examination. The 4, 6, 7, 8, 10, 12 and 14 hour old cultures (counted from the time of inoculation) were fixed with lactophenol. At every investigated point of time, 200 conidia in each of 6 parallel cultures were counted. Significance was calculated by the t-test.

Results and discussion

The temporal course of the germination percentage in the *Aspergillus* species examined is included in Table 1. It is to be seen that at the same point of time, the germination percentage is significantly higher in the large

Table 1

Time course in the germination percentage as a function of conidium number per surface unit in some Aspergillus species. (The data in this Table are the mean values of 6 parallel cultures. The germination percentage was determined on the basis of examining 200 conidia in each culture. For the definition of the small and the large inocula see the text.)

Time, in hours	*A. flavus* inoculum		*A. nidulans* inoculum		*A. niger* inoculum	
	Small	Large	Small	Large	Small	Large
4	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	44.52**	77.59**	3.63**	11.69**
7	2.54**	10.81**	81.01**	93.85**	37.02**	60.30**
8	9.40**	32.22**	100.00	100.00	84.58**	96.53**
10	51.73**	96.73**	—	—	100.00	100.00
12	65.55**	99.31**	—	—	—	—
14	100.00	100.00	—	—	—	—

** These values are significanthy different at the P=0.1% level.

than in the small inocula, that is, in the large inocula a germination inducing influence arises in the case of all three *Aspergillus* species. However, the final germination percentage is identical in both inoculum sizes.

According to these results it is safe to assume that the germination inducing effect in the case of large inocula was caused by the accumulation of germination inducing substances in the medium. These might have originated in the conidium directly, or they might have come into existence during germination.

What was said here also means that — at least under the conditions applied in my experiments — the phenomenon of self-inhibition could not be found. It is not likely that its cause is the complete lack of germination inhibiting substances from the spores. KRISHNAN et al. (1954), as well as GROVER (1964) describe that from the conidia of *Aspergillus niger* and *A. flavus*, respectively, inhibitory substances can be removed by washing with water. Therefore it is assumable that the phenomenon of self-inhibition in my experiments could not be demonstrated, because the inhibitory substances inducing it had been washed out when preparing the conidia. This, however, is a hypothesis that needs further confirmation.

As has been mentioned in the introduction, MEYRATH (1963), as well as MEYRATH and MCINTOSH (1965), point out that *Aspergillus oryzae* grows more rapidly in submerged fermentation and, in the last analysis, produces a larger quantity of dry material if the culture is carried out with large than with small inocula. In the filtrate of the large inocula, development stimulating substances could continuously be demonstrated during cultivation, whereas in the filtrate of cultures originating from small inocula inhibitory substances had been shown initially while stimulating substances at later points of time. However, it is by no means certain that these substances influence also the germination of the conidia. MEYRATH (1963) says that the size of the inoculum does not influence the lag period of *Aspergillus oryzae*, which, on the other hand, plays an important part in the germination of conidia.

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CHANGES IN THE ALKALOID PATTERN OF LATEX DURING THE DAY

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On the basis of investigation of 10 individuals each of our three poppy strains produced by individual selection, we established that during the day the alkaloid content of the latex in poppy varies to a great extent and in different patterns according to individuals. In the hours around midday and after midnight the total quantity of alkaloids, and also the proportion of the various bases, vary characteristically. So these points of time may be taken as the daily turning points of the alkaloid metabolism taking place in the latex of poppy.

The example of considerable individual qualitative and quantitative differences manifesting in the daily fluctuation of the alkaloid content of poppy latex testifies that in the plant the actual conditions of variations, as the daily periodicity, can be learned only on the basis of separate examinations of the individuals.

The investigation results obtained from 30 individuals of *Papaver orientale* also confirm the inferences the poppy.

Introduction

The daily variations in the alkaloid pattern of poppy have so far been investigated by SÁRKÁNY and DÁNOS (1957), HEYDENREICH and PFEIFER (1962) and FAIRBAIRN and WASSEL (1964); an investigation of *Papaver orientale* is not known. Since the methods of sampling in these poppy investigations were different, a comparison between the results obtained offers an excellent possibility of evaluating the efficiency of the various methods; thus when discussing our own results, we shall deal with the above investigations in detail. Concurrently we propose to discuss the more general bibliographical references of the question in connection with the biological importance of periodicity investigations of the individuals.

Material and method

The poppy was raised from isolated seeds of our strains, which were improved by individual selection from seed samples of botanical gardens in Bulgaria (A-strain), Morocco (B-strain), and Turkey (C-strain). The *Papaver orientale* L. plants belonged to a several year-old stock originating from a commercial seed, and on the basis of the ripe capsule pattern they represented preponderantly isothebaine chemotaxon. Examinations were carried out in two successive years in both plant species, by drawing latex from the developing capsules of 5 individuals of the two species each in one year, while in the other from those of 10 individuals

of each of the three poppy strains as well as from these of 30 *P. orientale* plants a few days after petal fall. The samples were taken every three hours and processed immediately, with the method described previously, by – approximative – quantitative thin-layer chromatography (VÁGUJFALVI, 1971).

Results and evaluation

(*a*) *Preliminary experiments with poppy*

The latex of 5 individuals was, investigated by sampling every 3 hours, to determine whether there is a daily variation in the alkaloidal content and pattern, and if there is, what are the characteristics of the daily periodical variations in the various alkaloids. The daily variations in the quantity of the various alkaloids of 4 individuals are shown in Fig. 1. (In this Figure the axes of codeine and thebaine have been shifted perpendicularly, in order to enable a better comparison with morphine; however, the unit-division of the axes remained unchanged so the quotient of alkaloid variations is not distorted.) It can be established from the Figure that:

1. The quantity of both the total and the individual alkaloids shows a fairly considerable fluctuation in latex during the day; the value of the maximum is in general about twofold of that of the minimum; however, there are considerable differences between the various alkaloids and also the plants individuals.

2. During the day the total alkaloidal quantity shows two maxima: one between 9 and 12 a.m. and the other during the hours around midnight; the minima appear in the morning (around 6 a.m.) and in the afternoon (3—6 p.m.). This course is, however, different according to individuals: in plant *3* the two maxima are of nearly identical value, in *1* and *2* the midday maximum is higher, while in *4* the night peak cannot even be recognized.

3. Variations in the alkaloids morphine, narcotine and papaverine during the day are fairly similar to one another; since both their quantities and the quotient of their variations surpassed these of the other two alkaloids, in essence these three bases determined the described daily variations in the quantity of alkaloids. Certain differences, however, can be observed also among these 3 compounds: the maxima and the minima do not always appear simultaneously, and there is deviation also in the intensity of changes in the various plants (e.g. in plants *1* and *2* the fluctuation in the quantity of narcotine, while in *3* and *4* that in papaverine is higher).

4. The daily variations in codeine and thebaine are entirely different from these described so far. In plant *2* they still form somewhat similarly as with morpnine, in *4*, however, the course of the curves is nearly antiparallel (at the time of the minimum in morphine content, the codeine and thebaine
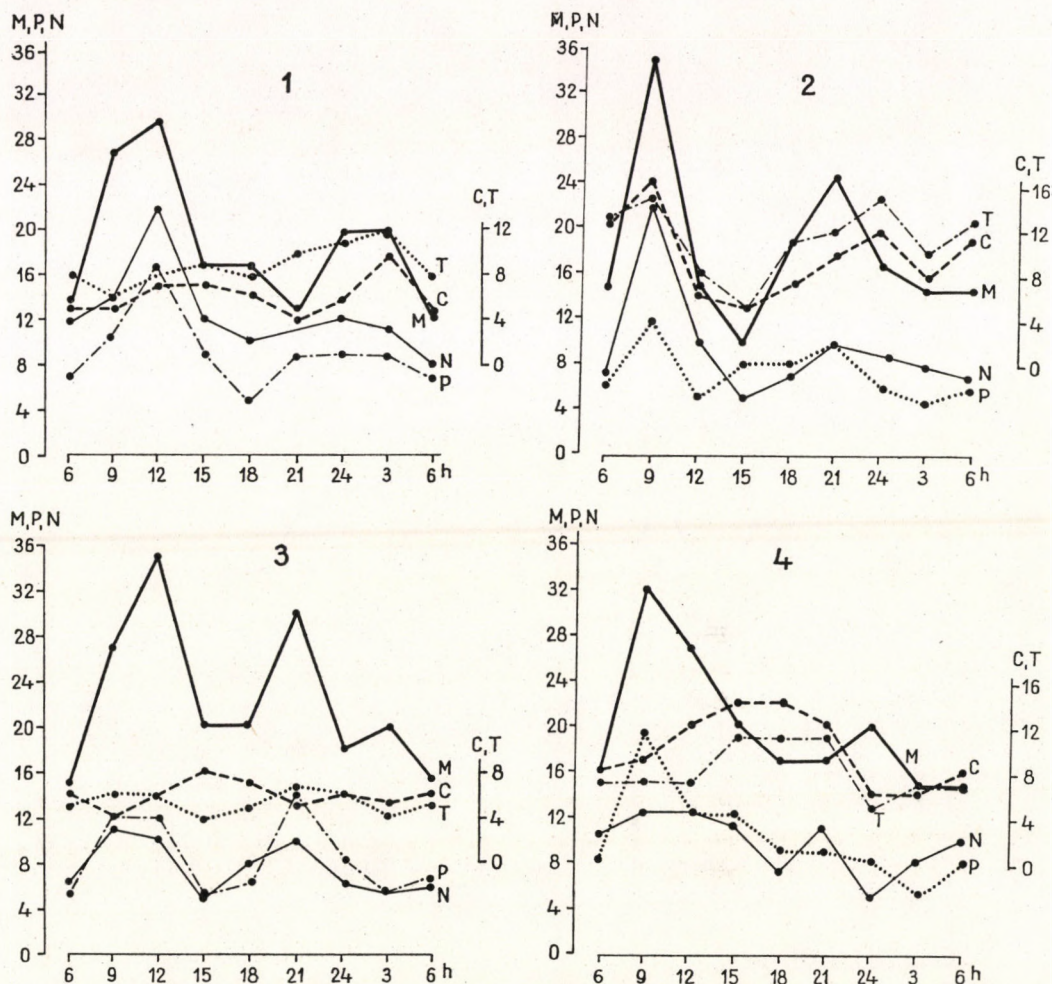
Fig. 1. Variation in the quantity of alkaloids in poppy latex during the day. M = morphine, C = codeine, T = thebaine, P = papaverine, N = narcotine, 1—4 = individuals

contents have their maxima), while in plants *1* and *3* there is hardly any characteristic variation.

5. A greater regularity seems to exist concerning the quotient of variations in codeine related to morphine: the morphine/codeine quotient is high in the forenoon and noon hours; then it decreases to its one third and one fourth, while in the night hours it again approaches — possibly reaches — the forenoon value. The codeine/thebaine quotient shows a variation of much lower rate and is less characteristic: its observable fluctuations are not parallel with the daily formation of either the morphine value ot that of morphine/codeine (Fig. 2).
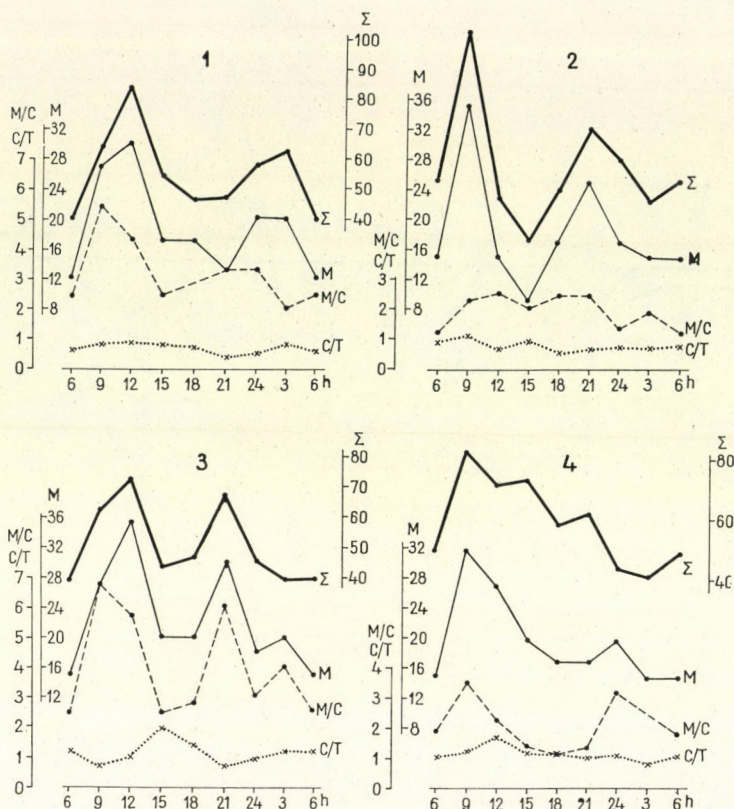
Fig. 2. Variation in the quotient of morphinane alkaloids during the day, in the latex of the 4 poppy individuals shown also in Fig. 1. Symbols as there; $\sum$ = total alkaloid

(*b*) *Investigation of 10 individuals of 3 poppy strains each*

To determine how the regularities that occurred in the preliminary experiments appear in plants of different origin (belonging to other strains), but of similar alkaloidal pattern, three our strains were investigated; while for a better understanding of the observed individual variations latex samples were drawn from 10 plants per strain every 3 hours. Of the results the daily variations in the total alkaloidal content of all 30 individuals are shown in Fig. 3, while in Fig. 4 (as an example) the quantity of the various alkaloids in 6 individuals, in Fig. 5 the variation in the quotient of morphinane alkaloids, and Fig. 6 the daily formation of the calculated average values of the three strains are shown. The results of the investigations are in full agreement with the data of the preliminary experiment: they have confirmed the inferences summarized in the 5 points above, and they allow some new inferences.

1. The individual variation of the daily formation of the total alkaloidal content (Fig. 3) is even greater than it seems on the basis of investigations of the 5 plants of the preliminary experiments. Beside the daily two curves showing noon and night maxima (e.g. A 1—5, B 1—2, C 1—4), also some appeared in which the first maximum (A 7, B 6), or the second (A 9, B 5—7, C 5—7), or both (A 6, B 3—4) maxima are blurred, or were absent, exhibiting thereby a transition, as it were, to the individuals where there appears only one peak — the one which in general is between 3—9 p.m. and only one minimum — around 12 midnight and 3 a.m. (A 10, B 7—10, C 8—10). These different curve types are distinguishable in the Figure presenting the formation of the total alkaloidal content in the plants of all three strains. Accordingly it can definitely be stated that the alkaloidal content of the poppy latex varies
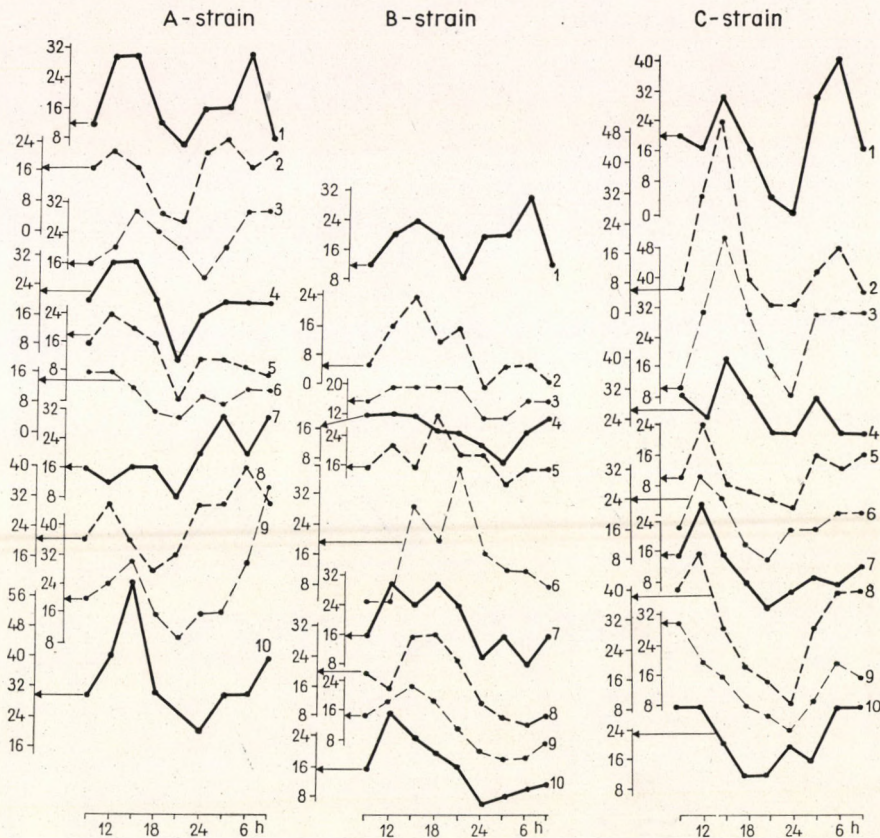
Fig. 3. Individual variability of the daily development of total alkaloidal content, in the latex of 10 individuals each (1—10) of three poppy strains (A, B, C). Alkaloid values: μg/mg latex dry weight

to a grat extent during the day and the variation if of a different character according to individual, and that these variations can be characterized by curves showing one maximum and two maxima as well as by a type which is a transition between the two.

2. On examining the daily variations in the various alkaloids of the 30 individuals we found that the quantities of morphine, papaverine, narcotine, and narcotoline — detectable in the A-strain — vary in essence parallel with one another in the latex even in the case of variations describable with different curve types. This is confirmed by the data of the 6 individuals with the different curve types in Fig. 4. If the various bases are summarized by alkaloidal types, the result implies that during the day the quantity of the 3 main alkaloidal types in the latex varies in a nearly identical way. This, on the other hand, suggests that the daily fluctuation in the quantity of the alkaloids of the poppy latex may primarily be a consequence of the variation in the mechanism activity functioning in the early stage of the alkaloid biosynthesis. The intensity in the development of the various alkaloidal groups does not vary, or varies very little, i.e. the quotient of the alkaloidal types primarily characterizing the various poppy strains is nearly constant during the day, and it manifests variations only during the development of the individual — as is suggested by our results published elsewhere (VÁGUJFALVI and TÉTÉNYI, 1973).

The fluctuation of the codeine and thebaine quantity — as is to be seen also in Fig. 4 — is completely different from that of the other alkaloids; beside the individuals providing almost constant codeine and thebaine values (e.g. A 1, but especially B 8), the course antiparallel
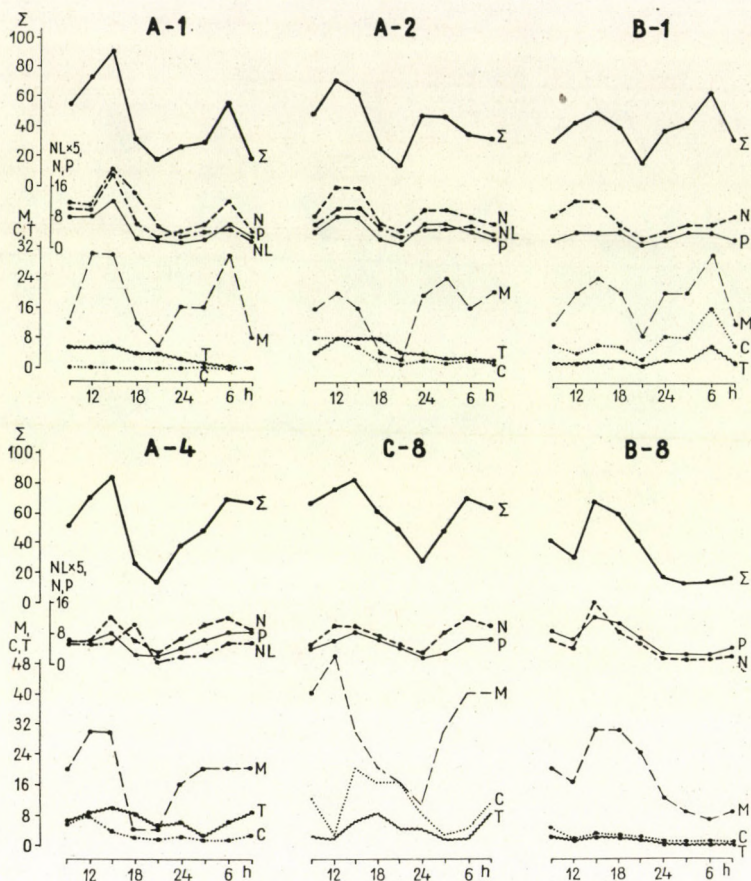
Fig. 4. Variation in the quantity of the various alkaloids during the day, in the latex of 6 individuals of those shown also in Fig. 3. Symbols used for alkaloids as in Fig. 1; NL = narcotoline, $\sum$ = total alkaloid

with morphine (which occurred in the preliminary experiment) manifested itself also here (C 8). This, on the other hand, suggests that not only the activity of the early stages of biosynthesis—mentioned previously—changes during the day, but also the activity of the systems determining the conversion between the morphinane alkaloids, and the changes are not identical. These changes can be followed on the basis of Fig. 5, where in the example of 11 individuals the daily variations of the morphine/codeine and codeine/thebaine quotiens (and, as a comparison, the data of morphine) are shown. As is to be seen the morphine/codein value reaches its maximum after a minimum before midnight, then by the morning it decreases again and remains at this low value in most of the individuals during the day; a noon maximum appeared only in a small number of individuals (C 1, C 8). The alteration of this proportion indicates the changes ensuing the demethylation of codeine into morphine (which is e.g. depending on the relative quantity of the methyl acceptor), but the relative speed of proteine formation and demethylation may also vary, and even a change in the activity of morphine conversion reactions, as indicated in the works by Fair-Bairn and El-Masry (1967, 1968), may be the evoking cause.

The change in the codeine/thebaine quotient and in the morphine/codeine quotient is reversed in time: the highest daily fluctuation of the codeine/thebaine value (rapid increase then decrease) is at the very time when the morphine/codeine quotient is nearly constant,
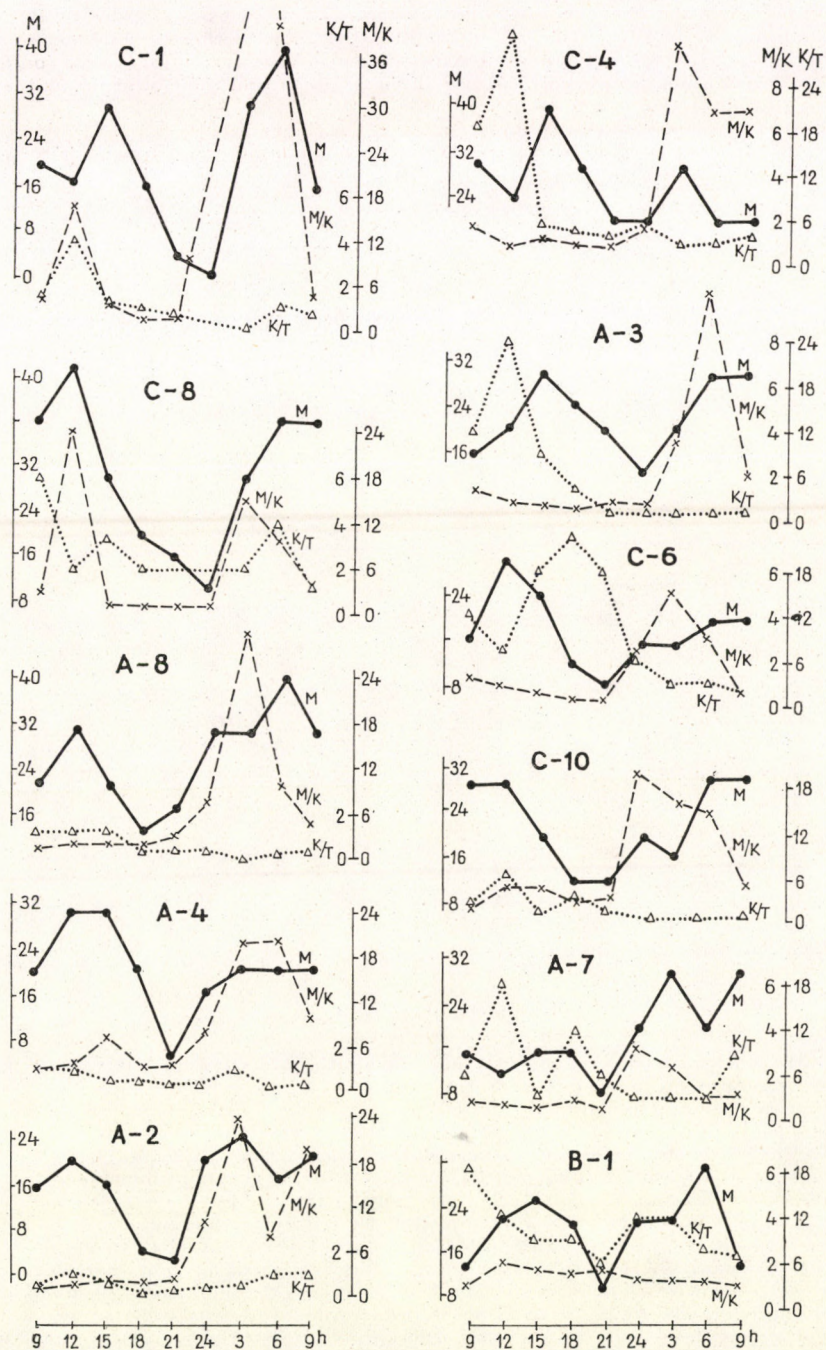
Fig. 5. Formation of morphinane alkaloid quotients during the day, in the latex of 11 individuals of these shown also in Fig. 3. Symbols as in Fig. 1

i.e. in the forenoon hours; at the time of great variation in the morphine/codeine value, on the other hand, namely in the second half of the day, the value of the codeine/thebaine ratio is unchanged. This is therefore not an antiparallel course and not the mathematical consequence of quotient calculation. This means that the intensity of the thebaine / codeine and codeine / morphine demethylation reactions is not maximal at the same point of time: the conversion into codeine is the most intense in the first half of the day, while its further conversion into morphine in the second half of the day. Hence in the hours around midday and after midnight
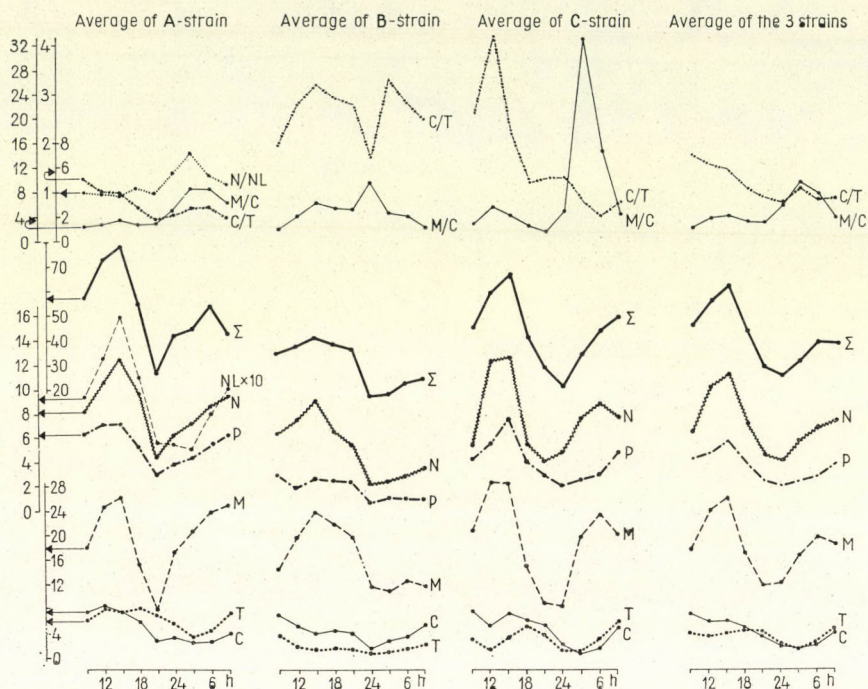
Fig. 6. Variation in the individual alkaloids their amounts and quotients given in the averages calculated separately and collectively of the 3 strains shown also in Fig. 3. Symbols as in Fig. 1

not only the general strengthening of the alkaloid synthesis occurs, but the various reactions of the conversions of morphine bases between themselves also become more intensive. Therefore these points of time may be considered the daily turning points of alkaloid metabolism occurring in the poppy latex.

In the 9 individuals of strain A there is, beside narcotine, also narcotoline of a detectable quantity, so we could investigate the fluctuation of these two members of the phtalidisoquinolines — differing from each other also only in the degree of methylation — during the day. As Fig. 4 shows in no less than 3 plants, there is a great degree of parallelism in the daily variation in the quantity of these two bases, and they also follow the variation of the total alkaloid quantity. Their calculated quotient shows a small and not characteristic daily variation on the individual level. Obviously, it is because of the increased inaccuracy of determination, deriving also from the small absolute quantity of narcotoline, that the formation of average values shows a recognizable trend in only 9 plants (Fig. 6). According to this, the narcotine/narcotoline quotient follows the variation in the morphine/codeine value well: thus, after midnight the quotient between the two morphinane bases shifts towards demethylation, while in the phtalidisoquinolines towards methylation. This apparent contradiction desappears if the general sequence of the biosynthesis in poppy alkaloids is considered (e.g. VÁGUJFALVI

and TÉTÉNYI, 1967), with the thebaine → codeine → morphine and the narcotoline → narcotine reaction directions. So it is not methylation or demethylation that should be considered in themselves, but the formation of the main paths in biosynthesis: demethylation in morphines, and methylation in phtalidisoquinolines. Accordingly, at the daily turning points of alkaloid metabolism the intensity of the functioning of the early stages of biosynthesis, determining both the general intensity of alkaloid development and the formation of the various alkaloidal groups, also changes and so does intensity of further formations within these groups.

3. On the basis of Fig. 6 one attempt might be made to learn whether, as regards the daily alkaloid changes in the various strains, there exist differences like those observed in the individuals. No considerable difference could be observed in the formation of the codeine and thebaine contents of the 3 strains, while the daily change in the quantity of total alkaloid, morphine, narcotine and papaverine as against the strain averages, shows no more difference than the daily second maximum emerging more expressedly also in strains A and C as in strain B. The data of the various plants show that this formation of the averages is a consequence of the fact that, among the individuals examined, plants with two maxima and those with one maximum as well as plants showing a variation of the "transitional type" occurred in varying proportions in the 3 strains.

The greatest differences among the strains appear in the proportion of the morphinane alkaloids. The morphine/codeine and codeine/thebaine values showed the greatest variation during the day in strain C and it was here that the contrast in time of the daily changes in the two values was the most expressed, i.e. the high night rise in the former proportion, and the high non rise in the latter proportion. The same formation can be observed in the A-strain, but the rate of the variation is much lower. (For example, the daily maximum of the morphine/codeine quotient here is about four times that of the minimum, while in the C-strain about its twentyfold.) The daily formation of the quotient average shows the least characteristic picture in the B-strain; this is mainly a consequence of the fact that codeine and thebaine were present in the smallest amount in this strain and so a small change in their absolute values results in a high distortion of the quotients. In the last analysis it can be said that the differences in the daily formation of the alkaloidal content among the strains examined are not great, and in general they derive from the fact that the quotients of the individuals exhibiting different. daily alkaloidal fluctuations in the strains are different. For a more accurate determination of the strain differences, the investigation of considerably more individuals would be required

The results allow the drawing of also a general conclusion that — in our opinion — shows far beyond the concrete problem examined and is of a general biological importance. As is clear from the foregoings — and as can directly be seen from the all alkaloids example in Fig. 3 — the daily change in the alkaloidal content of the poppy latex shows an extremely great variation according to individuals:

(1) The amplitude of the daily fluctuation is highly diverse; for example, the value of the daily maximum/daily minimum quotient is between 2 and 4 in certain plants, while in others it reaches even the 25—30 value; or, expressed in another way, it differs from the calculated daily average by less than $\pm 50\%$ in certain individuals (A 6, B 3, B 4, C 4), while in others it reaches $+100\%$, and even 250%, as well as $-90-100\%$ (C 1, C 2, A 9);

(2) As has already been pointed out, also the type of the daily variation in the alkaloidal content shows a considerable variation: daily two maxima appear in a considerable part of the individuals, while in others only one maximum, and in certain individuals the fluctuation may be considered a transitional type; the two maxima may also be of identical extent, although the first maximum is usually higher, but it may also occur that the second peak surpasses the first. These are the actual, the biologically realized variations, for the determination of which micro methods like our latex sampling technique are necessary. Despite the fact that the daily periodicity of a number of processes enacted in the plants has already been examined and determined (the summary of which is e.g. SWEENEY, 1963; SOLLBERGER, 1965; BÜNNING, 1967), these experiments were performed by the analysis of average samples. The project had, in most of the cases, a technical character: to establish the rate of variation so that the resultant error might be considered in subsequent investigations; or the aim was to determine the most suitable point of time for sampling in order to eliminate the error caused by the daily variation. It happened frequently that the solution was required for a definite, practical problem e.g. the determination of the best "cutting time" of the crop, to harvest the maximum of active principles. Beside the investigation of extensive research work was done on the individual variability of various biologico-biochemical phenomena (true, primarily in human and animal subjects, but work in the field of plants is also considerable: WILLIAMS, 1956). The combined investigation of two factors, i.e. the examination of individual variability of rhythm phenomena were completely lacking. For the investigation of the characteristics determinable by analyses there is, however, no technique at our disposal permitting several daily sampling

of one individual without damaging the plant to an extent of influencing the results. This were possible at the most in individuals of large volume (e.g. in trees); here, however, the gradients within the individual might be of an order to preclude the possibility of taking several assumably identical samples. It was only in exceptional cases that rhythm phenomena were examined in individuals (e.g. GUNAR and al. 1958). In the course of our investigations, first the daily formation of the prochamazulene content of *Matricaria chamomilla* was examined by plant individual, and in the paper reporting on the results of that work (VÁGUJFALVI and TYIHÁK, 1961) we already pointed out the importance of investigations of individuals. We said then: to the earlier ... "investigations — in order to elaminate individual differences — samples were used that were obtained a great number of plants and weighed 800—1000 g. However, with this the possibility of determing the actual variations within one inflorescence was also excluded". The results then showed that the fluctuation in the daily prochamazulene content within individuals was considerably higher (70—80%) than could be observed on the basis of average samples up to that time (20—25%). The deviation is of an even greater extent in poppy alkaloids if information from individuals is compared with that furnished by "average samples" (through the mathematical averaging of analysis values in individuals, i.e. homogenized in an "ideal way"). The daily maximum/daily minimum quotient value of the total alkaloidal quantity in the calculated average of the 3 strains lies between 2.4 and 3.4, i.e. the deviation from the daily average is about $\pm 50\%$, therefore as much as the smallest variation that occurred in the individuals: the cause of this is that the actual quantitative differences are blurred, since the maximum and the minimum in the individuals did not emerge at the same point of time. The individual examples of the high qualitative and quantitative differences appearing in the daily fluctuation of the alkaloidal content in the poppy latex indicates that the qualitative and quantitative conditions of changes, such as the daily periodicity, actually enacted in the plant, can be understood only on the basis of investigation of the individuals; our results published elsewhere (VÁGUJFALVI, 1968) testify that the same refers to the variations occurring during ontogenesis, so our inferences hold for both of the two most important rhythm phenomena.

Our results relating to the daily variations of alkaloidal content need to be compared with the data in literature. As outlined above, the sampling technique determines the efficiency of the investigations. It is interesting that the various investigations conducted so far related to three different levels. SÁRKÁNY and DÁNOS (1957) and HEYDENREICH and PFEIFER (1962) determined the alkaloidal pattern of the various parts of the plants: during the day they analyzed groups of certain numbers of individuals, i.e. different plants appeared in every sample, by elaborating the whole plant, FAIRBAIRN and WASSEL (1964) examined the repeated latex sample of a given stock (20—30 individuals); our method, on the other hand, made it possible to analyze also the patterns of the latex samples drawn every 3 hours from the individuals separately. Accordingly, the information content obtainable from the investigations is also of 3 levels. In our own work we succeeded in determining the qualitative and quantitative differences between individuals in the daily variation of the alkaloidal pattern of latex, as well as the more general regularities, characteristic of strain and species, manifested beyond the individual difference. In the average sample, drawn from several identical individuals of the given stock, these differences not only failed to appear, but an average is not always suitable for the determination of the general characteristics either. This is so in FAIRBAIRN and WASSEL's work, too: they publish the values of daily variation in morphine content obtained from 8 investigational series, but only one (T_5) of them shows a daily course seemingly characteristic — the authors illustrated only this curve — while the others show only smaller or greater, somewhat irregular "fluctuation". (On the basis of the values included iu their tables, we have drawn the curves of the morphine values from the 8 series; see Fig. 7.) No similarity can be recognized among the curves, not even in their trend; for example, between 8 and 12 a.m. there occur maxima (T_5, B_1), a minimum (T_1), constancy (T_2-July 13), continuous decrease (T_3, T_2-July 14), and irregular fluctuation. HEYDENREICH and PFEIFER have in no case obtained a regular variation; in their paper, containing a tremendous amount of data, even they themselves desisted to draw any inferences. In his summarizing paper, PFEIFER (1962) writes about their work as follows: "The daily rhythm of the various alkaloids is different, similarly to the case of the various organs where periodicity is not uniform either. Besides, the daily rhythm depends also upon the developmental state of the plant and also upon external conditions." This, of course, is possible, but our primary aim is the determination of not these differences, but of the basic laws; a reference to only the differences is an admission of the fact that no interconnections could successfully be established. In the last, all what can be inferred from the foregoing is that the alkaloids change during the day to a considerable extent in the plant (for example, daily variations obtained concerning morphine: HEYDENREICH and PFEIFER -30 and $+16\%$; FAIRBAIRN and WASSEL -51 and $+96\%$ as a maximum; for a comparison,
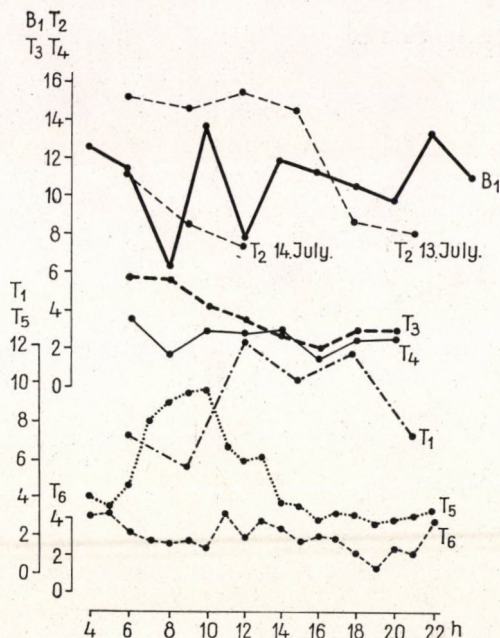
Fig. 7. Variation in the quantity of morphine in poppy latex during the day compiled from the data of FAIRBAIRN and WASSEL (1964); B_1, T_1—T_6 = investigational series

our own extreme values are —100 and +250%; these values are percentage of the deviation from the daily average); further, that the changes of the various alkaloids are different (according to FAIRBAIRN and WASSEL, the direction of the change in codeine and thebaine runs counter to that of morphine). These data do not contradict our own results, it is only that their information content is much smaller than that obtained from our individual examinations.

In connection with the daily formation of the alkaloidal content of the poppy latex, one more question should be answered. It may rightly be raised whether the quantitative differences occurring in alkaloids are not merely the consequences of concentration changes in latex, possibly also in daily periodicity? A satisfactory answer can be given on the basis of FAIRBAIRN and WASSEL's data: it is not so. These authors, as they indeed found certain variations in the dry matter content of the latex during the day, calculated the alkaloidal values related also to the fresh and dry weights of the latex: the curves of morphine and thebaine, given for these two basis of reference, are practicaly identical, at least far within the limit of error (FAIRBAIRN and WASSEL, 1964; Figs 1 and 2). The observed changes in alkaloid content are therefore the consequences of the variation in the intensity of alkaloidal synthesis and of the possible periodical transport of the alkaloids within the plant during the day, while the qualitative (i.e. alkaloid quotient) changes derive from the differing rate of conversion from one alkaloid into another and of their possible further conversion (into non-alkaloids), therefore the consequences of daily variations occurring in the biologico-biochemical processes of alkaloidal metabolism. The fact that these processes may indeed involve considerable variations in activity is confirmed also by the isotopic examinations of FAIRBAIRN and al. (1964), FAIRBAIRN and EL-MASRY (1967).

(c) *The daily variation in the alkaloidal pattern in the latex of Papaver orientale*

Concurrently with, and using the same methods in the poppy investigationes described above, first then 30 individuals were also studied. In Fig. 8 the results from the preminilary experiment concerned with the variation in
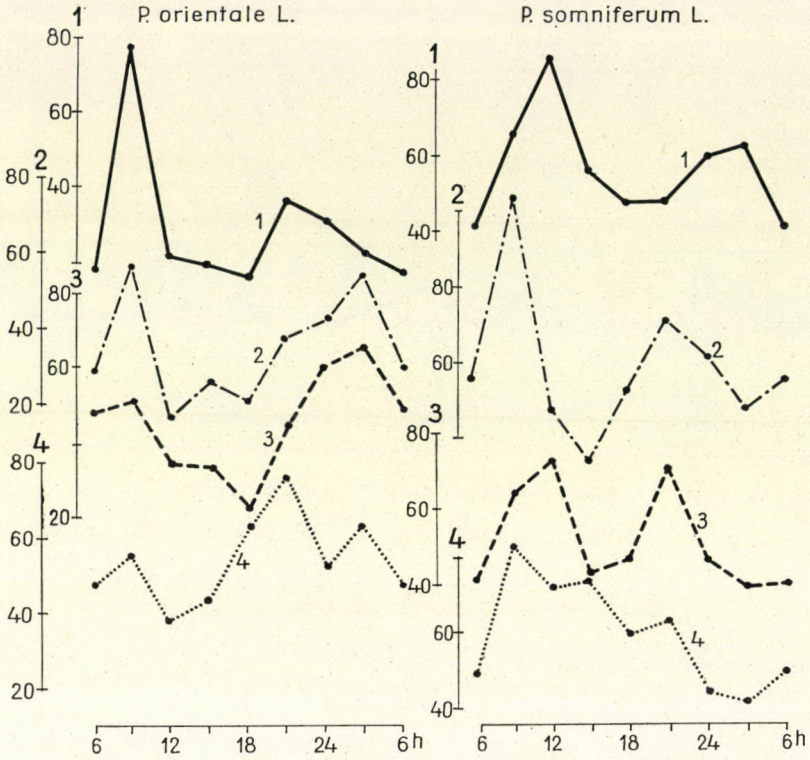
Fig. 8. Variation of total alkaloid content in the latex of *Papaver orientale* L. and *P. somniferum* L. during the day. 1—4 = individuals
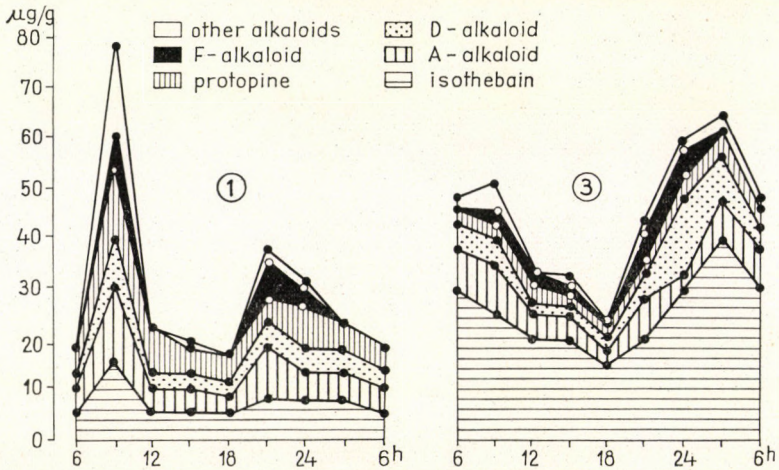
Fig. 9. Variation of alkaloid pattern in the latex of two *Papaver orientale* L. individuals during the day

the total alkaloid content of the latex of the 4 individuals, in Fig. 9 the daily variation in the alkaloid pattern of the two individuals of extreme types (one with isothebaine, and one "without major alkaloid", i.e. containing 4 alkaloids in a nearly identical quantity are shown). In Fig. 8 also the diagrammatic comparison between data related to the 4 individuals of the preliminary experiment in poppy is given. Quite conspicuously, the total alkaloidal content of the latex in the two species runs a fairly similar course during the day; it can be observed that the daily two maxima and the differences between the individuals exist in the same way. The above inferences were confirmed by some 3000 date of the 30 individuals examined in the succeeding year since, however, they implied nothing new, their publication in detail would be superfluous.

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INVESTIGATION OF AUXIN-INDUCED GROWTH IN TOBACCO CALLUS CULTURE

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The developmental processes in the callus culture of *Nicotiana tabacum*, kept in sterile conditions, were examined by measuring some of the parameters of metabolism. On the basis of the measured data (fresh weight and dry weight variations, cell number, cell weight, RNA and total protein content, ribonuclease-, peroxidase- and auxin oxidase activity) of the auxin-treated 34 and 50 day old callus culture, it could be established that:

1. Growth changes according to an optimum curve as a function of auxin concentration; the best development was induced by the 0.25—1.00 mg/l concentration;
2. Growth of the culture was concurrently associated with increasing water uptake higher dry matter production and changes in cell size;
3. A correlation exists between the auxin-induced development of the short-period (34 days) culture and the long-period (50 days) culture and the measured low ribonuclease activity. The activity of the well-growing variants appeared always low, and that of the variants with inhibited development emerged always higher;
4. A significant RNase activity decrease appears already under the effect of a very short period (few hours) of auxin treatment;
5. The variations in the RNA and the total protein contents suggest that the auxin effect extends also to these metabolic areas of our subject;
6. The changes in the activities of peroxidase and auxin oxidase enzymes suggest intricate interconnections. Peroxidase and auxin oxidase may fulfil their functions as a uniform system of enzymes, through their various isoenzymes.

From the point of view of the effect mechanism of auxin playing a leading role in development, the changes in the nuclease level and its possible regulatory role were considered especially important. Our data supplement the great number of observations relating to auxin, and they also allow the formulation of a new hypothesis.

The series of investigations also prove that, in the research of metabolic regulation in plant cells and tissues, the technique of culturing tissues is a well-applicable and useful method with many inherent possibilities.

Introduction

Growth physiology is a chapter discussing one of the most complicated processes of plant physiology. Although early research into the process began already at the end of the last century, there are still a whole series of problems awaiting solution. Today we know that in the regulation of this process phytohormones play the leading role. Their effects are reflected by recent data from various aspects. Less verified knowledge is available concerning the mechanism of these materials (auxins, cytokinins, gibberellines, ethylene, abscisic acid, etc.). The aim of our experiment was to follow the effect of

auxin (β-indolil acetic acid = IAA) by applying a modern physiological method (sterile tissue culture), possibly with an investigation of a large scale metabolic background. To accomplish this, we registered growth by measuring several metabolic indices; in addition — for the sake of considering the processes of senescence — two incubation periods (34 and 50 days) were employed. In the interests of our aim, also methodological problems had to be overcome, since tissue culture as a special object raised new demands against our methods.

Today the conception that there is an interrelationship between the effects of auxin and the metabolic processes of nucleic acid is well founded (SILBERGER and SKOOG 1953, BRIQUET et al. 1967, KEY and SHANNON 1964, BENDANA et al. 1965). The interconnection with protein metabolism is similarly close (FANG and YU 1965, NOODEN and THIMANN 1963). The investigation of the interrelationship between auxin and senescence also seems to be important in general. This again leads to the field of nucleic acid and protein metabolism (PILET 1969, SACHER 1967). According to most recent data and also to our results, enzymes (the nucleases) decomposing nucleic acid may play an important role in the effect mechanism of auxins (CALDOGNO et al. 1968, PILET and BRAUN 1970, TRUELSEN 1967). On this basis, the evaluation of growth required the measuring of the increase in fresh weight, variations in dry material content cell number, the quantity of RNA and total protein, the activity of ribonuclease-, peroxidase- and auxin oxidase. The data obtained allowed to submit a newer one in the rank of various conceptions formulated on the mechanism of action (ARMSTRONG 1966, FARKAS 1968, MERKYS et al. 1971, PILET 1961, SARKISSIAN 1968).

Material and method

In the experiments, *Nicotiana tabacum* callus culture was cultivated on a modified variation (VETTER 1972b) of the nutrient used by MURASHIGE and SKOOG (1962). The culture vessels were used after an overpressure sterilization at 0.7—0.8 atm for 45 minutes, and then incubation for 3 days. An explantation of 200 mg fresh weight was placed in each of the tubes. These were kept at 18—24°C, in the conditions of natural light variations (day and night phases).

The aim of the experiments was to investigate the auxin effect, therefore the applied basic nutrient did not contain β indole acetic acid. It was difficult to answer the question whether overpressure would not result in the decomposition of auxin when preparing the nutrient for the variants. Concerning this question, literature has no uniform views, or the authors do not report on this concern. Therefore, we staged also experiments wherein a buffer, containing auxin of a known quantity, was tried by autoclaving at various atmospheres (0.25—1.00), then samples were taken from the individual variants. The auxin content of the samples was determined by the GORDON—WEBER reagent to be described below, then compared with the auxin content of the not autoclaved control. According to the data the quantity of auxin remained unchanged at each pressure examined. For detecting possible products of decomposition a chromatographic test was also developed (PROCHÁZKA 1961). No decomposition product was found, so it could be satisfactorily stated that auxin proves to be heat stable during the preparation of the nutrient medium.

Knowing the incubation time, we characterized the increase in fresh weight by a daily increase (mg/day). The determination of dry material content was carried out on the

basis of our method described previously (VETTER and MARÓTI 1971), and given in percentage of the fresh weight.

The determination of the cell number was made on the basis of BROWN and RICKLESS's method (1950). Samples weighing 25 mg each were fluffed with chromic acid. From the cell suspension thus obtained, the cell number was determined by dropping up in a BÜRKER chamber, in three repetitions per sample, then the cell number was related to 1 g fresh weight tissue. With the aid of the weight and cell number data, the fresh and dry weights of cells were calculated (for 10^{-4} mg/cell and 10^{-5} mg/cell units).

The determination of ribonuclease activity was carried out from the homogenate of samples weighing 250—250 mg each, on the basis of a method described previously (VETTER 1972a). Activity was characterized after incubation of a given period and temperature, on the basis of increase in the optical density (OD) measurable at 260 mμ. This change is caused by the decomposed RNA, while the non-decomposed nucleic acid was previously precipitated and removed by centrifugation.

The determination of peroxidase activity was carried out on the basis of a method (described previously; cf. VETTER 1972a) developed for tobacco tissue culture. In the case of the method applying guayacol substrate, the activity is expressed by relating the intensity increase during a given unit of time, to 1 g fresh weight the brown colour due to the enzyme activity.

The measuring of the auxin oxidase (IAA oxidase) activity posed the greatest problem in the method to be applied. The main cause lies in the enzyme functioning in complicated inhibiting activating conditions. This fact poses a great number of methodological problems, indicated also by the respective publications (MEUDT 1970, SEQUEIRA and MINEO 1966). The various parameters of the reaction in general (time, temperature, the presence of activators, oxigen supply, light or dark) and also the means of extraction are fairly different. Our preliminary experiments attempted to develop a method allowing determinations which required little material and no special purifying stages. In our method an acetated homogenate prepared for the determination of ribonuclease was used. The composition of the reaction mixture is as follows: 0.75 ml phosphate puffer (pH = 6.0 0.017 M), 0.75 ml Mn^{++} solution (freshly prepared, 0.1 mg $MnCl_2$/ml), and 0.25 ml from the supernatant of the homogenate. The reaction started with the addition of the auxin (0.25 ml IAA solution, 225 μg/ml), then the solution was shaken on a Vibroterm machine at 30°C for 4 hours. The reaction was stopped by adding 2 ml of GORDON—WEBER reagent (GORDON and WEBER 1951), then colour intensity measured at 530 mμ after 60 minutes. The rate of auxin decomposition was characterized with the quantity of auxin decomposition by the tissue of unit weight during a unit of time (μg decomposed auxin/g fresh weight/hour).

The RNA and protein contents of the samples were determined on the basis of PILET and BRAUN's method (1967); the RNA content with orcinol reaction, on the basis of the ribose content of the fraction obtained in alcalic hydrolysis, while the protein content with FOLIN reaction (LOWRY et al. 1951), which previously proved fairly reliable. The assay of the determinations was carried out with the aid of standard curves for ribose (on RNA), and bovine serum albumin (protein). The data are given in μg RNA/g fresh weight, μg RNA/g dry weight, and in mg protein/g fresh weight, mg protein/g dry weight values.

The mathematical evaluation of the experimental series was carried out on the basis of our earlier work (VETTER and MARÓTI 1971). According to these, the individual parameters are characterized by the mathematical mean value, the error, and the arithmetical mean value expressed in percentage of the control.

Experimental results

I. The effects of auxin on the ribonuclease activity of tobacco tissue in short incubational experiments

On the basis of our earlier preliminary experiments, tissue pieces of identical weight were treated for identical periods with a solution containing auxin, then the RNase activity of the tissues was determined and related to the control which was treated with distilled water (Table 1). The results of our

Table 1

The influence of auxin treatments on the ribonuclease activity of tobacco callus tissue ($\overline{x}$ = arithmetical mean; s = error; % = per cent of arithmetical mean)

Auxin concentration (mg/l)		Incubation time: 2 hours — Ribonuclease activity (OD_{260})	Incubation time: 4 hours — Ribonuclease activity (OD_{260})
	$\overline{x}$	0.561	0.583
Control	s	0.032	0.012
	%	100.0	100.0
	$\overline{x}$	0.624	
0.01	s	0.005	—
	%	111.0	
	$\overline{x}$	0.543	
0.1	s	0.002	—
	%	96.8	
	$\overline{x}$	0.676	0.596
1.0	s	0.011	0.015
	%	100.9	75.8
	$\overline{x}$	0.566	0.442
2.0	s	0.011	0.015
	%	100.9	75.8
	$\overline{x}$	0.501	0.461
8.0	s	0.027	0.030
	%	89.3	79.0
	$\overline{x}$	0.411	0.410
16.0	s	0.021	0.012
	%	73.3	70.3
	$\overline{x}$		0.398
32.0	s	—	0.022
	%		68.3
	$\overline{x}$	0.850	
64.0	s	0.050	—
	%	151.2	
	$\overline{x}$		1.06
128.0	s	—	0.05
	%		181.8

Fig. 1. **Changes in the ribonuclease activity of tobacco callus tissue caused by auxin treatment. Incubation time: 2 hours [abscissa: auxin concentration (mg/l); ordinate: ribonuclease activity, in per cent of untreated control]**
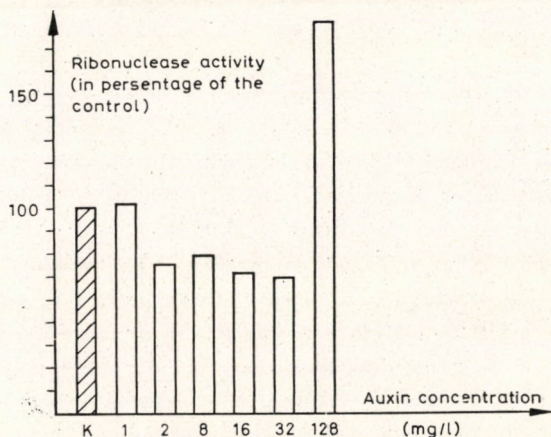
Fig. 2. **Ribonuclease activity of callus tissue, after auxin treatment. Incubation time: 4 hours [abscissa: auxin concentration (mg/l); ordinate: ribonuclease activity in per cent of untreated control]**

first incubational experiment are shown in Fig. 1. After a 2-hour treatment we examined the effect of the auxin treatment. According to the data, during this period a decrease in the RNase activity could be observed in the case of 16 mg/l concentration, while a concentration of 64 mg/l considerably increased the activity. The other variants seemed in essence ineffective, or the differences that occurred were not considerable. On the basis of experiences gained from this series, the incubation time was increased to 4 hours, the two smallest concentrations (0.01; 0.1 mg/l) were left out, while the concentration series was supplemented with a 128 mg/l variant. According to the results of the series (Fig. 2), a 25% activity decrease was caused already by the 2 mg/l

concentration. Similar, or higher, is the effect with 8, 16, 32 mg/l concentrations (i.e. 21; 30; 32% decrease). On the other hand, the greatest concentration increased the activity to 181% in comparison with the untreated control.

Our experiments showed that in a relatively short time (a few hours) on incubation, considerable alterations occur in the activity of callus RNase, and that these activities are under the effect of the exogen auxin treatment regulating some enzyme level. In general, the concentrations, which from the point of view of increase in the tissue culture, are of the most favourable effect, cause here a well demonstrable nuclease activity decrease (around 1—2 mg/l concentration). Obviously, auxin can be effective in this experiment only if the tissue can absorb it. This could be achieved by the use of a higher auxin concentration than that applied in experiments involving a longer period (several weeks).

II. Investigation of the growth-inducing effects of auxin in 34 and 50 day experiments

The object of the experiment was a multi-parameter investigation, the auxin effect, consisting of two parts. In the first series of experiments the relevant parameters were assayed after an incubation period of 34 days, while in the second series after 50 days of incubation. In the first series the tissues were cultivated in nutrient mediums of 0.0; 0.25; 1.0; 2.0; 8.0; and 16 mg/l auxin concentrations. The data are to be found in Tables 2 and 3.

Growth. The data are illustrated in Fig. 3. The prominent stimulation by the 0.25 mg/l concentration variant in growth is conspicuous, while the 1 and 2 mg/l concentrations also considerably increased the daily growth. The fresh weight increment occurring at the two highest concentrations in comparison with the control and also the other variants shows inhibition. It must be mentioned here that the values of the daily growth are data partly
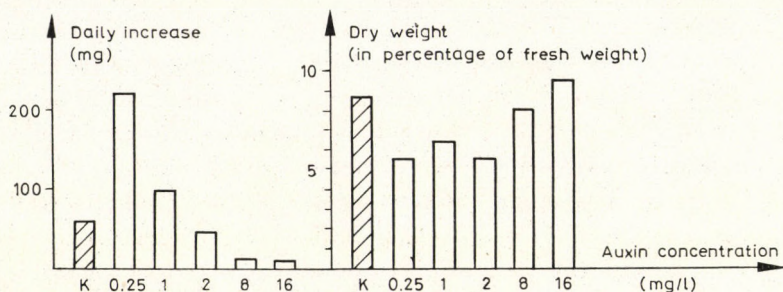
Fig. 3. Changes in growth and dry weight of tobacco callus tissue, cultured for 34 days [abscissa: auxin concentration (mg/l); ordinate: growth (mg/day), and dry weight in per cent of fresh weight]

Table 2

The effect of auxin on the parameters of growth, dry weight, cell number, fresh and dry weights of cells, RNA- and protein contents, ribonuclease, peroxidase and auxin oxidase activities of tobacco callus culture. Incubation time: 34 days ($\bar{x}$ = arithmetical mean; s = error; % = per cent of arithmetical mean)

Metabolism indicators		Auxin concentration (mg/l)					
		control	0.25	1	2	8	16
Growth (mg/day)	$\bar{x}$	42	224	97	45	7.2	5.8
	s	10	39	36	26	4.0	2.7
	%	100.0	530	210	108	16	13
Dry weight (in per cent of fresh weight)	$\bar{x}$	8.75	5.41	6.42	5.64	8.17	9.82
	s	0.73	0.59	0.76	0.03	1.12	0.49
	%	100.0	61.8	73.3	64.4	93.3	112.2
Number of cells ($\times 10^6$/g fresh weight)	$\bar{x}$	1.48	1.21	1.81	1.90	2.19	2.60
	s	0.29	0.17	0.27	0.39	0.34	0.41
	%	100.0	81.7	122.3	128.0	147.9	175.6
Fresh weight of cells ($\times 10^{-4}$ mg/cell)	$\bar{x}$	6.7	8.2	5.5	5.2	4.5	3.8
	s	1.3	1.1	0.8	1.0	0.7	0.6
	%	100.0	123	82	78	67	58
Dry weight of cells ($\times 10^{-5}$ mg/cell)	$\bar{x}$	5.9	4.4	3.5	2.9	3.7	3.7
	s	1.6	1.0	0.9	0.6	1.0	0.7
	%	100.0	75	60	50	63	63
RNA content (μg/g dry weight)	$\bar{x}$	1786.7	2298.0	2452.7	2448.7	1909.0	2520.0
	s	155	227	123	224	179	108
	%	100.0	128.6	137.3	137.1	106.8	141.1
RNA content (μg/g fresh weight)	$\bar{x}$	156.4	124.3	157.5	138.1	156.1	247.5
	s	12.8	12.3	7.8	23.3	14.9	19.7
	%	100.0	80.6	102	89	101	160
Protein content (mg/g fresh weight)	$\bar{x}$	3.4	2.02	2.5	1.4	3.9	4.0
	s	1.1	0.1	0.2	0.1	0.2	0.8
	%	100.0	59.2	74.1	42.8	115.2	118.4
Protein content (mg/g dry weight)	$\bar{x}$	38.9	37.3	39.4	25.9	48.1	41.1
	s	13.5	2.2	2.9	2.5	2.4	8.4
	%	100.0	98	101	66	123	105
Ribonuclease activity (OD_{260})	$\bar{x}$	0.618	0.386	0.383	0.358	0.401	0.483
	s	0.065	0.012	0.060	0.008	0.025	0.030
	%	100.0	62.4	61.9	57.9	64.8	78.1
Peroxidase activity (OD_{420}/g fresh w./min)	$\bar{x}$	10.1	13.7	11.2	12.4	14.4	20.2
	s	1.5	2.1	2.5	2.0	0.75	1.7
	%	100.0	135	110	122	142	200
IAA oxidase activity (μg decomposed auxin/g fresh weight/hour)	$\bar{x}$	280.9	201.9	201.8	123.4	29.3	1.8
	s	59.8	30.2	27.9	40.9	7.3	1.5
	%	100.0	71.8	74.0	44.4	10.4	0.6

of a relative character; in using them, the unsteady rate of development should not be forgotten. Nevertheless, we consider the data of the daily growth values satisfactory for our aims.

Dry weight. According to Fig. 3, showing the variations in dry weight content, the three variants exhibiting the greatest growth have a dry

weight content of 30—40% less than the control, while in the case of the two variants of the highest concentration the resulting value is nearly identical with that of the control. Apparently, the fresh weight increment induced by the auxin is associated with water uptake, while in the case of the increasing variants the water uptake is lower, and the dry weight variations are not considerable.

Cell number, cell weight. The variation in the cell number related to the fresh weight in grams is shown in Fig. 4. According to this the number of cells increases with the increase in auxin concentration;
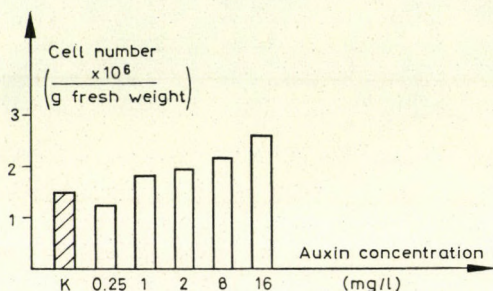
Fig. 4. Number of cells of tobacco callus tissue, cultured for 34 days [abscissa: auxin concentration (mg/l); ordinate: number of cells ($\times 10^6$) g fresh weight]

at lower concentrations the variation is of 20—25%, while in the case of the two high concentrations the increase is of 47% and 75%. In comparison with the data relating to growth, it can be stated that the cell number of well developing variants is lower than that of the less developing variants. The fresh weight increment, the formation of the dry material content, the variation in cell number do not reflect in every respect the changes occurring in the size of the cells. This is why we calculated the fresh and dry weights of the cells (Fig. 5). The data refer to the correlation that a considerable increase in cell weight occurs in well-growing variants; hence we are dealing here with cells of a high waters content and large size but fewer in number; beginning with the concentration 1 mg/l the fresh weight of the cells decreased rapidly, at the highest auxin concentration to almost their half. The tendency is less conspicuous in the dry weight of the cells: the dry weight of the cells of the variant with the greatest growth is the largest in comparison with the other, auxinic variants, but even so it is still less than that of the control.

RNA content. According to the data, the RNA content related to fresh weight shows no considerable deviation among the individual variants. However, in the variant with the highest concentration, an increase of 60% occurs. According to the data related to the unit of dry material, the RNA content is higher in all variants with auxin. It seems, therefore, that the pres-

ence of auxin results in a higher RNA level, though this appears considerable when related to dry matter only.

Protein content. Determining the protein content with Folin reaction, the results indicate that when related to fresh weight, the quantity of protein decreases in the best growing variants (0.25; 1.00 and 2.00 mg/l), and only in the case of the highest auxin concentration was it possible to determine a stimulation to some extent (15%). If the protein content is related
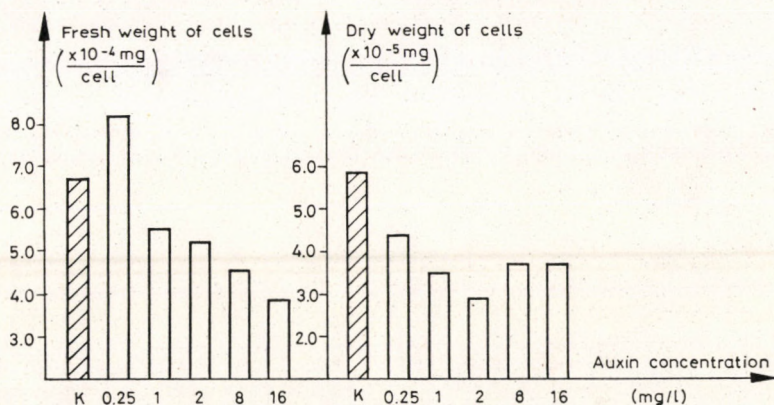
Fig. 5. Fresh and dry weights of tobacco callus cells, cultured for 34 days [abscissa: auxin concentration (mg/l); ordinate: fresh weight of cells ($\times 10^{-4}$ mg/cell), and dry weight of cells ($\times 10^{-5}$ mg/cell)]

to dry weight it can be considered unchanged (apart from a prominent value) although the two highest values are given by the two variants of the highest concentration. By comparing the RNA contents with the protein contents it may be stated that the variation of the auxin induced RNA level is more expressed, at least after a 34-day incubation.

RNase activity. Of our data relating to enzyme activity, the ribonuclease data seem to show the clearest interconnection (Fig. 6). All variants treated with auxin showed a low activity in comparison with the control. On the other hand, the activity is lower only by 22% when under the effect of the highest — 16 mg/l — concentration of auxin. It seems therefore that auxin treated tissue pieces, continuing an undisturbed metabolism for a somewhat longer time, show a lower RNase activity, otherwise the growth is associated with a lower hydrolitic enzyme activity.

Peroxidase activity. According to our data (Fig. 7), every auxin treated variant showed a greater activity and the increase in concentration resulted in ever higher activity values (at a maximum, the value doubled as related to the control tissue). It is more difficult to answer in what way this depends on the concentration. It is possible that within certain limits
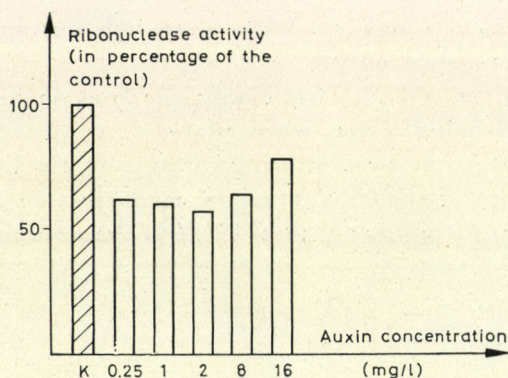
Fig. 6. **Ribonuclease activity of tobacco callus tissue, cultured for 34 days [abscissa: auxin concentration (mg/l), ordinate: ribonuclease activity (in per cent of control)]**
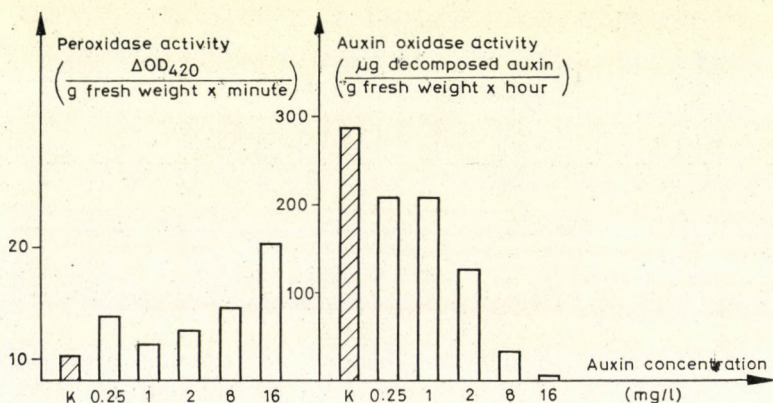
Fig. 7. Peroxidase and auxin oxidase activity of tobacco callus tissue, cultured for 34 days [abscissa: auxin concentration (mg/l); ordinate: peroxidase activity (OD_{420} change/g fresh weight/min) and auxin oxidase activity (μg decomposed auxin/g fresh weight/hour)]

this has no considerable importance, what is essential is whether there has been auxin present in the nutrient medium or not.

IAA oxidase activity. As a function of increasing concentration, highly decreasing activity values were obtained (Fig. 7). This decrease is of 30% in 0.25 1 mg/l and concentrations, while high concentrations almost completely reduce the activity measurable with our method. Apparently, the more auxin is present in the nutrient — strangely — the less the activity of the decomposing enzyme system.

In the second series of our experiments we investigated the growth, and the metabolic indices measured in connection with it after a longer incubation time and using fewer concentration variants. The 16 mg/l variant was left

Table 3

The effect of auxin on the parameters of growth, dry weight, cell number, fresh and dry weights of cells, RNA- and protein contents, ribonuclease, peroxidase and auxin oxidase activities of tobacco callus culture. Incubation time: 50 days ($\bar{x}$ = arithmetical mean; s = error; % = per cent of arithmetical mean)

Metabolism indicators		Auxin concentration (mg/l)				
		control	0,25	1	2	8
Growth (mg/day)	$\bar{x}$	168.5	212.3	119.5	51.7	22.5
	s	22.3	64.6	50.0	10.2	13.5
	%	100.0	125.9	70.9	30.6	13.3
Dry weight (in per cent of fresh weight)	$\bar{x}$	5.37	5.79	5.23	6.14	6.18
	s	0.41	0.37	0.40	0.44	0.10
	%	100.0	107.4	97.3	114.3	115.0
Number of cells ($\times 10^6$/g fresh weight)	$\bar{x}$	2.25	1.07	1.35	2.21	2.34
	s	0.57	0.10	0.26	0.17	0.10
	%	100.0	47.5	60.0	98.0	104.0
Fresh weight of cells ($\times 10^{-4}$ mg/cell)	$\bar{x}$	4.44	9.30	7.40	4.52	4.27
	s	1.11	0.86	1.45	0.34	0.18
	%	100.0	220.4	168.5	101.4	97.5
Dry weight of cells ($\times 10^{-5}$ mg/cell)	$\bar{x}$	2.3	5.4	3.8	2.7	2.6
	s	0.75	1.12	1.48	0.44	0.15
	%	100.0	228.2	168.7	120.7	110.6
RNA content (μg/g fresh weight)	$\bar{x}$	132.6	114.1	129.1	121.7	127.2
	s	10.0	14.5	8.6	3.4	1.3
	%	100.0	86.4	97.8	92.2	96.3
RNA content (μg/g dry weight)	$\bar{x}$	2469	1970	2468	1969	2058
	s	186	250	164	55	21
	%	100.0	79.8	99.9	79.7	83.3
Protein content (mg/g fresh weight)	$\bar{x}$	3.30	5.30	5.83	3.19	3.36
	s	0.80	0.70	0.62	0.45	0.53
	%	100.0	175.4	193.2	105.6	111.2
Protein content (mg/g dry weight)	$\bar{x}$	57	93	105	52	54
	s	14.8	12.0	11.8	7.3	8.6
	%	100.0	163.2	182.3	91.7	95.5
Ribonuclease activity (OD_{260})	$\bar{x}$	1.02	0.37		0.37	0.48
	s	0.19	0.02	—	0.06	0.03
	%	100.0	36.4		36.1	46.6
Peroxidase activity (OD_{420}/g fresh w./min.)	$\bar{x}$	14.6	9.3	10.4	7.6	10.4
	s	2.2	0.43	1.0	0.8	2.7
	%	100.0	63.6	71.2	52.0	71.2
IAA oxidase activity (μg decomposed auxin/g fresh weight/hour)	$\bar{x}$	50.8	87.5		305.9	234.8
	s	16.2	23.2	—	65.0	20
	%	100.0	162.3		610.1	470.0

out, while the incubation was continued for 50 days. The data are to be found in Table 3.

Growth. When comparing the values of the fresh weight increment (daily growth) with one another; it will be found that the effect of 0.25 mg/l auxin is unambiguously stimulating, while the other concentra-

tions have an inhibiting effect as compared with the control. In comparison with the similar values obtained in the preceding (34 day) series (Fig. 3), a very good correspondence occurs, for example in the 0.25 mg/l concentration: the daily increase is 224 and 212 mg in the case of 34 and 50 day incubations, respectively. On the basis of the dry weight data it seems that the differences between the variants tend to diminish during longer incubation periods.

Cell number, cell weight. The number of cells related to the unit of fresh weight considerably decreases (by 52%) in the best growing variant, then by increasing (in the two highest auxin concentrations) it reaches
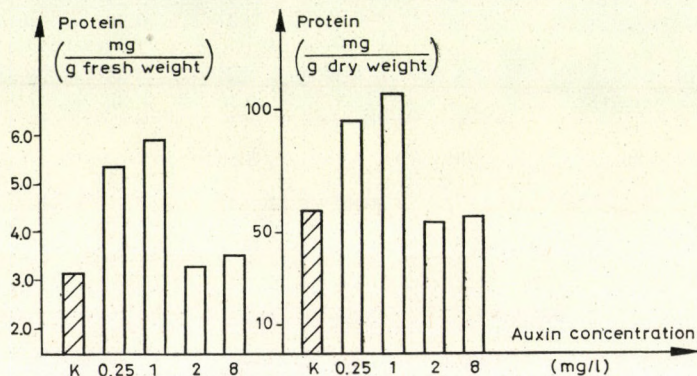
Fig. 8. Protein content of tobacco callus tissue, cultured for 50 days [abscissa: auxin concentration (mg/l); ordinate: protein content (mg/g fresh weight, and mg/g dry weight)]

the level of the control. It can be stated that the optimal auxin quantity decreases the cell number during the 50-day incubation period, similarly as during the 34 days. According to the cell weight data, two variants — 0.25 and 1 mg/l — have a considerably higher cell weight (120 and 68% higher), while the two high concentrations have no effect (+1 and —3% variations). The same tendency prevails in relation to the cell dry weights. Our data confirm the inference that the weight increment occurring under the auxin effect is in correlation with cells of high water content and probably greater size.

RNA content. No essential deviation from the control, or among the variants, was indicated by the RNA — whether given on a fresh weight basis, or with reference to dry weight.

Protein content. The quantity of total protein content varies according to a characteristic optimum curve as a function of concentration (Fig. 8), related to fresh weight. The extent of stimulation is 75 and 93, (5 and 11%) according to the increasing auxin concentration. A correlation of similar character occurs in relation to the dry weight. As could be seen in the case of 50-day-old cultures, the auxin treatment induced a considerable increase

in the protein content, and this effect is strongly dependent on the auxin concentrations, for the 2 and 8 mg/l dosages did not alter the protein level. Another important fact is that the increased protein content is characteristic of the best growing variants, i.e. the stimulation of growth coincides with a higher protein content.

RNase activity. According to the data of the RNase activity of the tissue, the activity of the variants grown in the nutrient containing auxin is substantially lower than that of the control (the data of the 1 mg/l
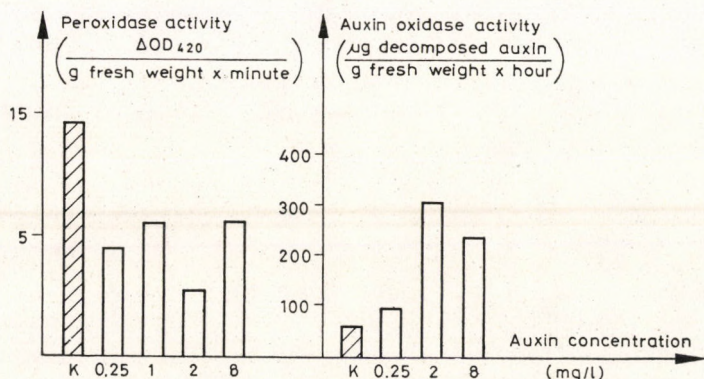
Fig. 9. Peroxidase and auxin oxidase activities tobacco callus tissue, cultured for 50 days [abscissa: auxin concentration (mg/l); ordinate: peroxidase activity (OD_{420} change/g fresh weight/min.), and auxin oxidase activity (μg decomposed auxin/g fresh weight hour)]

variant is omitted from the table). The resulting tendency confirms the inference drawn from the 34-day experiment series, i.e. that the presence of auxin causes a decrease in the RNase activity.

Peroxidase activity. The variation in the activity (Fig. 9) as related to the 34-day series showed a deviating tendency in this series. The data of all variants are namely considerably smaller than that of the control. The role of concentration, at least in the interval applied is again not clear; it is the presence of auxin that may be of importance. It can be stated that the enzyme level of peroxidase changes under the effect of auxin differently in the 50-day culture than in the 34-day series. However, in the metabolism processes of the 50-day culture senescence processes also play a part.

Auxin oxidase activity. Similarly to the peroxidase activity also IAA oxidase showed deviating activities (Fig. 9), because the IAA decomposing ability of the tissues substantially increased in the variants. In the two highest concentrations this increase is 4—6 times higher than the activity of the control tissue. Therefore this enzyme, too, behaved wholly differently in callus culture series cultivated for shorter than for longer periods. What is

interesting and remarkable is that the changes in the enzyme levels are of opposite signs: a high peroxidase level occurs with a low IAA oxidase level and vice versa.

Discussion

Auxin-induced growth processes were in the focus of our investigations made on tissue cultures of tobacco callus. The experiments were intended to determine primarily the correlations in growth lasting for a longer time, while an experiment of short incubation period was also conducted in relation with the metabolic index. On assaying the data of the experiments, an attempt was made to describe, through the parameters examined, and to evaluate, from the point of view of the mechanism of action, the effects of auxin.

The process of plant growth is of a complex character, a complicated series of changes involving the whole metabolism. First we always measured the increment, one of the easily measurable quantitative characteristics of growth, in fresh weight in the 34 and 50 day experiments. We could establish also with this subject that the inducing effect of auxin shows an optimum curve in the function of concentration. The optimal concentration interval is between 0.25—1.0 mg/l (Fig. 1). On the basis of our data it is also clear that one of the consequences of the inducing effect of auxin is the increasing water uptake. This is the origin of the increase in size and weight of the cells. Could it be that the motor of the growth stimulating effect is simply the increasing water uptake? That this is not so can be proved also by the fact that the dry material content of the cells also increased under the effect of the optimal auxin content. This is especially indicated by the data of the 50-day culture.

In the auxin-induced processes, the various processes of nucleic acid and protein metabolism play an important part. According to the first observations, auxin treatment increased the total nucleic acid content of the stem tissue of tobacco (SILBERGER and SKOOG 1953). In general, the auxin-induced development can be inhibited with actinomycin D and chloramphenicol (BUCZEK 1969). The question is obvious: to which RNA fraction or fractions of the cell does the auxin extend effect? The answer cannot yet be considered unambiguous today, for increase in the synthesis of both the ribosomal RNA (KEY and SHANNON 1964) and the mRNA (MASUDA, TANIMOTO and WADA 1967) could be demonstrated in various objects.

In the regulation of the nucleic acid metabolism a leading role is attributed to the function of the nuclease enzymes. The investigation of the nucleases started as a biochemical problem, but their physiological role became ever more interesting. On the basis of our data (Figs 1, 2, 6; and the Tables)

we investigated the importance of ribonuclease activity from the viewpoint of growth processes. It can be stated that the tissue manifests a lower RNase activity under the effect of auxin treatment. This effect also depends on the concentration, for the high concentration considerably increases the activity. The variations obtained in both the 34 and 50 day experiments were of the same trend as those received in the experiment lasting for a few hours only According to our data, the auxin effect can be described so that it induces an RNase activity decrease already in a short time. On the other hand, the decrease in hydrolytic activity clearly promotes the anabolic processes. In the same way, it became clear also in the case of tissues grown on a nutrient substrate, that well developing tissue shows a lower activity. As for the older tissues, the fact of senescence inhibition also counts in interpreting the auxin effect. In the effect of auxin we consider, on the basis of our data, the developing lower hydrolytic enzyme level, a fairly important factor regardless of the age of the object. On the basis of our investigations we regard the data obtained in the case of various objects as confirmed. For example, an RNase activity decrease under the effect of auxin was demonstrated in wheat coleoptile pieces and pea stem segments (TRUELSEN 1967), lentil root cells (PILET and BRAUN 1970) and also in the bean endocarp (SACHER 1969). Other but more indirect data confirm our statement concerning growth and RNase correlation (MARÓTI 1969).

The tracing of the growth processes was supplemented with the investigation of the levels of two other enzymes, viz. peroxidase and auxin oxidase, which raised a series of new problems. The data of the cultures indicated an increase in the peroxidase activity in one case (34 day series), while in the other (50 day series) they indicated a decreasing effect (Figs 7 and 9). The variations in the two experimental series were thus divergent.

Considering the physiological role of the peroxidases, it would be very difficult to point out the most important role in which it plays the part of the chief regulator. Undoubtedly, in certain cases it functions as a terminal-oxidase in the process of respiration, but in general this role is very uncertain (FARKAS 1968). Newer data attribute to peroxidase a role in the biosynthesis of lignin. It is noteworthy that peroxidases are found in nearly every tissue, implying some function of universal importance.

Data are known that point out in the tissue culture of Pelargonium stem an increase in the peroxidase activity due to IAA in a short period experiment (50—150 hours) (LAVEE and GALSTON 1968). A similar increase in activity occurred in tobacco stem tissue in experiments taking 2—3 weeks (GALSTON et al. 1968). When separating electrophoretically the peroxidase, which is known to consist of several isoenzymes, it turned out that along with the increase in total activity the activity of some isoenzymes decreased, while that of other isoenzymes increased, under the effect of auxin.

Other data (YONEDA, 1970) suggest that certain peroxidase isoenzymes possess an IAA oxidase activity. Although there are still many authors who write about a distinct IAA oxidase enzyme, we believe that the same enzyme system is responsible for the activity of both the peroxidase and the IAA oxidase. True, the isoenzyme (s) performing the IAA oxidation functions in fairly complicated inhibitory — activiting conditions — and this is also the cause of the methodological problems. It is not without interest that our results show two opposite tendencies as to the IAA oxidase activity. In the case of the 34-day series (Fig. 7) it seemed that the substrate (auxin) strongly decreased the measurable total activity. This phenomenon is seemingly incomprehensible, since the higher substrate concentration usually exerts a counter effect. The phenomenon might be explained as a consequence of some other phenomena as well, as for example that of the presence of some inhibitory substance, but this would require definite corroboration.

In the case of the older culture the pattern was reversed (Fig. 9); a higher substrate concentration caused a higher measurable total activity. Recent data (LEE, 1971) concern a report on the investigation of the IAA decomposing activity, regulated by auxin and cytokinins, of the IAA oxidase isoenzyme in 20—30 days old tobacco tissue cultures. Groups of isoenzymes stimulated at low and at high auxin concentrations were separated. A correlation was described between the optimal growth concurrent with isoenzymes activated at a low concentration, and growth inhibition coincident with isoenzymes functioning at a higher concentration. In all probability therefore different isoenzymes per concentration play the leading role but we could investigate functioning only on the level of total activity.

The trend shown by the comparison of peroxidase and IAA oxidase activities is very interesting. A higher peroxidase activity is associated with a lower IAA decomposing activity (34-day experiment), while a low peroxidase activity occurred with a higher IAA decomposing ability (50 day experiment). In the light of the new data described previously, we may assume the existence of a uniform enzyme system that fulfils its peroxidase and IAA oxidase functions according to a varying ratio (through its various isoenzymes), depending on auxin treatment and age. As to the ratio of the measurable total activities, a younger tissue (Fig. 7) can decompose the smaller quantity of auxin which — from the point of view of growth — seems to be logical.

After a survey of our data, we have to answer the question about the components of the effect, and whether we can formulate some conception as to the effect of auxin. Concerning the process of growth in the case of the tobacco callus tissue we have been able to establish that it consists of a series of changes ranging over the whole metabolism of the tissue, and that it comes into existence as a result of a summation of these processes. Phytohormones play an important part in its regulation. From the point of view

of mechanism of action we considered rather important the stimulation of nucleic acid and protein metabolism, and the changes occurring at the enzyme level. On the basis of our data, the regulatory path may have an essential role. Of the conceptions submitted in literature, the data relating to activity changes induced by auxin seem to be confirmed, and our hypothesis might be called "nuclease" theory. The growth coordinating role of peroxidase — IAA oxidase enzyme system, uniform to our belief, should also be emphasized. The changes occurring in the water regime are also significant.

It goes without saying that growth processes are connected with a great number of other metabolic processes, not examined in our experiments. Only the completion of the entire research project and the synthesis of the results will lead to a complete understanding of the complicated metabolic background of growth, provided that the discussion is in essence about the realization of genetically fixed, determined possibilities. In this process the function of the regulator is fulfilled by the activating-inhibitoring system of the phytohormones.

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STUDIES ON THE EFFECT OF THIOUREA, I. A. A., AND GIBBERELLIC ACID ON THE GERMINATION OF THE DORMANT SEEDS OF CELOSIA ARGENTEA L.

By

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Seeds of *Celosia argentea* stored dry for 60 weeks were found to possess dormancy. 3% Thiourea has been found to promote germination up to 33% in light. An interaction of thiourea (3%) and ascorbic acid (10 mg%) gives maximum germination (62%) under light conditions, while under dark incubation maximum germination (65%) is obtained with an interaction of GA 100 ppm and 1% NH_4NO_3. Two roles of ascorbic acid have been observed: the synergism with thiourea in stimulating germination and the antagonism to the stimulatory effect of thiourea in light. Inorganic nitrogenous substances have been found to accelerate the germination promoting activity of GA.

Introduction

Amen (1966) regards seed dormancy as an adaptive mechanism of growth cessation which often confers upon some species a selective advantage in distribution and abundance. In India very little work has been done on the nature of dormancy and the factors overcoming this dormancy in the seeds of Rajasthan desert plants. The present study aims to investigate the effect of thiourea, ascorbic acid, I. A. A. and GA, both individually and jointly, on the germination of the seeds of *Celosia argentea*, an erect glabrous annual herb abundant especially on cultivated ground. The plant flowers during the end of the rainy season.

Material and methods

Seeds of *C. argentea* collected from plants growing around Udaipur (24° 35'N lat. and 75° 49'E long.) and stored dry in stoppered glass bottles in dark for 60 weeks were used for experiments. The seeds were germinated in Petri dishes on filter paper, kept moist by distilled water. The source of light was an incandescent bulb of 60 W, fixed at a distance of 30 cm from dish level. The energy of light at dish level as recorded by radiometer, was 1.65×10^4 erg/mm²/sec.

The seeds were immersed (in distilled water or solutions) in dark at 25°C for 8 hours and incubated at 30°C. The entire set with four replications of 50 seeds was repeated twice. Germination was recorded for a period of 4 days.

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Observations

The effect of thiourea, ascorbic acid and I. A. A. on germination

Observations on the rate and per cent germination of *C. argentea* seeds pretreated with the above compounds are presented in Figs 1 and 2. Data indicate that
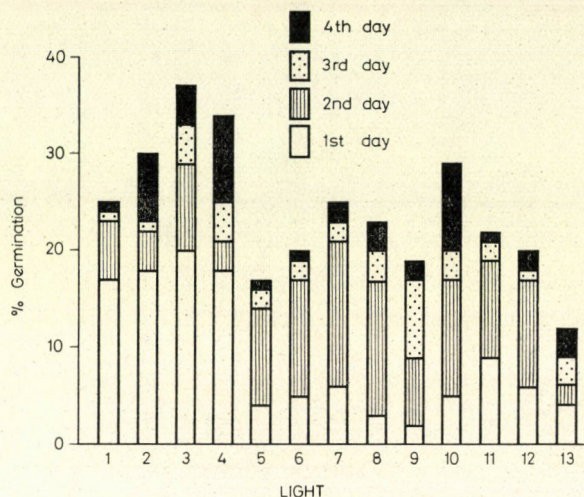
Fig. 1. Effect of thiourea, ascorbic acid and I. A. A. pretreatment on the germination of *C. argentea* seeds incubated in light

1 Thiourea 1%
2 Thiourea 2%
3 Thiourea 3%
4 Thiourea 4%
5 Ascorbic acid 10 mg%
6 Ascorbic acid 25 mg%
7 Ascorbic acid 50 mg%
8 Ascorbic acid 100 mg%
9 I. A. A. 10^{-9} M
10 I. A. A. 10^{-8} M
11 I. A. A. 10^{-7} M
12 I. A. A. 10^{-6} M
13 Control

a) The slight negatively photoblastic nature and the presence of dormancy in the seeds are apparent from the control set, since the maximum germination obtained is only 16% and it is higher in the dark.

b) Thiourea (3%) shows maximum speed and per cent germination both under light (37%) and dark (46%) conditions. Further increase in the concentration of thiourea retards germination. It is further clear from the observations that thiourea does not alter negatively photoblastic nature of these seeds.

c) Under light conditions ascorbic acid (50 mg %) has been found to show a maximum germination of 25%, while under dark incubation concentration of only 10 mg % is observed to produce maximum germination (31%). Further increase in concentration has been found to retard germination.

d) Maximum germination under light (29%) and dark (26%) conditions is obtained with I. A. A. concentrations of 10^{-8} M and 10^{-7} M, respectively. The observations further indicate that the treatment with I. A. A. reverses the negatively photoblastic nature of these seeds.
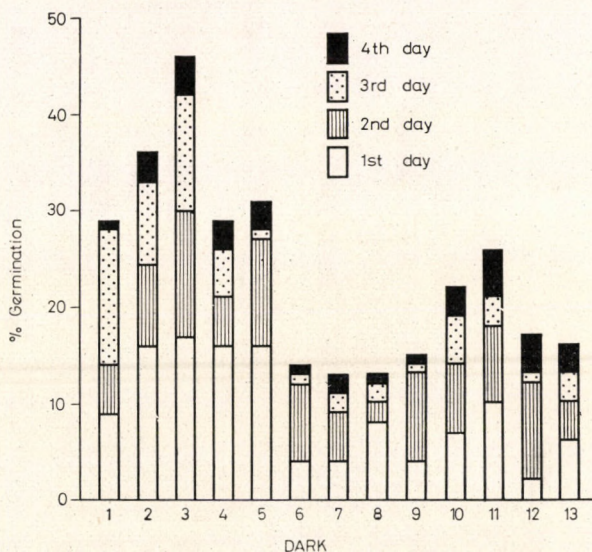
Fig. 2. Effect of thiourea, ascorbic acid and I. A. A. pretreatment on germination of *C. argentea* seeds incubated in dark. Symbols as in Fig. 1

Interacting effect of thiourea and other compounds on germination

The interacting effect of ascorbic acid and I. A. A. with thiourea (3%) on germination of *C. argentea* seeds is presented in Fig. 3. The observations indicate that

(i) Under light conditions interaction of thiourea with ascorbic acid (10 mg %) gives maximum speed and germination (62%). Further increase in the concentration of ascorbic acid retards germination so much that a concentration of 100 mg % becomes inhibitory. Under similar conditions the interaction of thiourea with I. A. A. (10^{-8} M) gives a maximum germination of 52%.

(ii) Under dark incubation in an interaction of thiourea and ascorbic acid the speed and per cent seed germination increases with the increase in the concentration of ascorbid acid, the maximum germination (60%) being obtained at a concentration of 100 mg %. Under similar conditions an interaction of thiourea with I. A. A. suggests that an I. A. A. concentration of 10^{-6} M proves inhibitory, that of 10^{-7} M has no effect, while 10^{-8} M and 10^{-9} M concentrations prove promoting. The maximum germination (54%) is obtained at 10^{-8} M concentration of I. A. A.
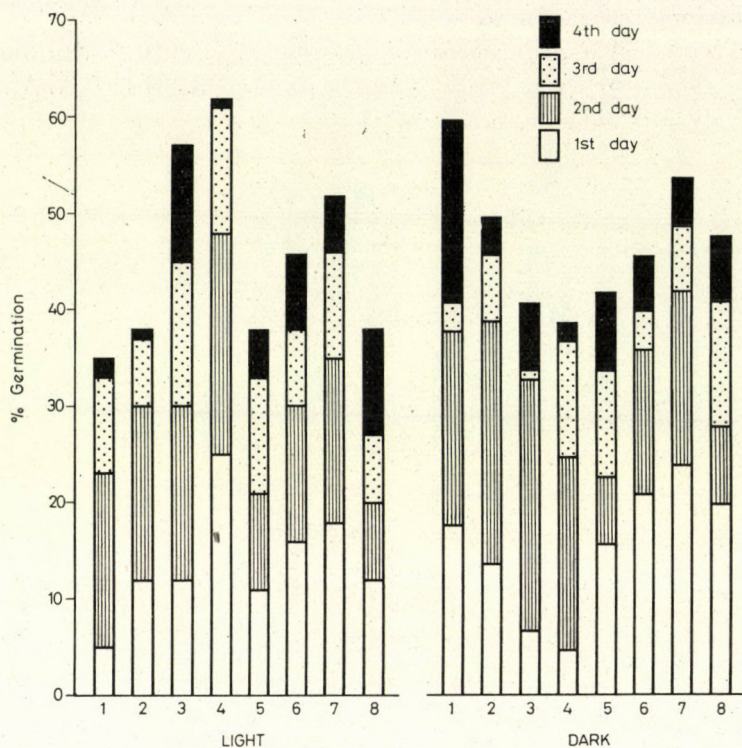
Fig. 3. **Effect of interaction of thiourea, ascorbic acid and I. A. A. on the germination of *C. argentea* seeds**

1 Thiourea 3% + Ascorbic acid 100 mg%
2 Thiourea 3% + Ascorbic acid 50 mg%
3 Thiourea 3% + Ascorbic acid 25 mg%
4 Thiourea 3% + Ascorbic acid 10 mg%
5 Thiourea 3% + I. A. A. 10^{-6} M
6 Thiourea 3% + I. A. A. 10^{-7} M
7 Thiourea 3% + I. A. A. 10^{-8} M
8 Thiourea 3% + I. A. A. 10^{-9} M

Effect of GA on germination

Observations on the germination rate and percentage of *C. argentea* seeds pretreated with GA of different concentrations are presented in Fig. 4. The observations suggest that pretreatment of seeds with GA shows a stimulatory effect. It is further observed that with an increase in the concentration of GA 100 ppm, both rate and per cent germination increase, reaching maxima (26% and 25% in light and dark, respectively) with a 100 ppm concentration. GA concentration of 200 ppm is found to retard germination.
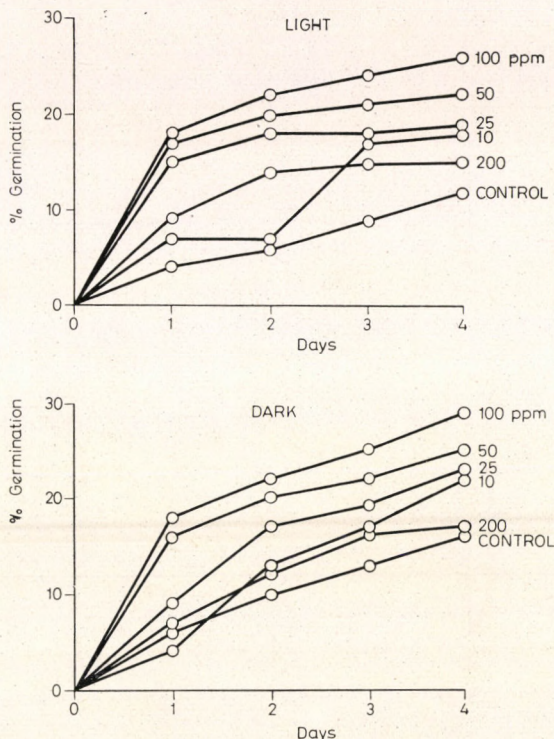
Fig. 4. Effect of GA pretreatment on the germination of *C. argentea* seeds

Increation of GA and inorganic nitrogenous compounds

Experimental results in the study of the effect of nitrogenous compounds (KNO_3, NH_4NO_3, NH_4Cl and $(NH_4)_2SO_4$ individually as well as in association with GA, on the germination of *C. argentea* seeds are recorded in tables 1 and 2. It is observed from table 1 that both KNO_3 and NH_4NO_3 are themselves capable of improving germination in these seeds. Under light incubation 2% concentrations of both substances give maximum germination (KNO_3 — 26%; NH_4NO_3 — 36%) while a concentration of only 1% is most effective in dark, giving 34% and 53% germinations in KNO_3 and NH_4NO_3, respectively. The data also suggest that enhancement of GA activity increases with an interaction of both these nitrogenous substances. An interaction of GA (100 ppm) with 2% concentrations of both these salts give maximum germination (KNO_3 — 53%, NH_4NO_3 — 58%) in light, while in dark maximum germination (KNO_3 — 49%; NH_4NO_3 — 65%) is obtained with only 1% concentration of these salts.

Table 1

Effect of potassium nitrate and ammonium nitrate on germination of C. argentea seeds in presence and absence of GA. (Results are in progressive % seed germination)

Days	KNO_3							
	Light				Dark			
	1	2	3	4	1	2	3	4
GA alone (100 ppm)	18	19	23	26	18	22	25	29
GA + 1% salt	28	39	45	45	27	42	48	49
GA + 2% salt	25	40	40	53	18	22	26	37
GA + 3% salt	17	22	24	31	22	29	32	34
Water	4	6	9	12	6	10	13	16
Salt alone 1%	9	11	12	18	27	32	33	34
Salt alone 2%	21	23	23	26	17	19	19	22
Salt alone 3%	18	19	19	19	19	19	20	22

Days	NH_4NO_3							
	Light				Dark			
	1	2	3	4	1	2	3	4
GA alone (100 ppm)	18	19	23	26	18	22	25	29
GA + 1% salt	29	43	50	54	30	48	60	65
GA + 2% salt	30	45	50	58	37	44	47	49
GA + 3% salt	20	34	41	44	19	33	44	45
Water	4	6	9	12	6	10	13	16
Salt alone 1%	18	25	28	30	21	41	50	53
Salt alone 2%	33	35	35	36	27	41	42	43
Salt alone 3%	19	25	26	29	29	34	35	41

Observations presented in table 2 suggest that both NH_4Cl and $(NH_4)_2SO_4$, although by themselves very weak in inducing germination of *C. argentea* seeds, are effective in enhancing the germination inducing activity of GA. NH_4Cl has been found to be comparatively more effective than $(NH_4)_2SO_4$.

Discussion

Very poor germination, even with a postripening period of 60 weeks, suggests the presence of some dormancy block in these seeds. Ability of thiourea to break dormancy in seeds (MAYBER et al. 1958, VYAS and AGARWAL, 1971) has also been recorded in the present investigation. Thiourea at a concentration

Table 2

Effect of Ammonium Chloride and Ammonium Sulphate on germination of C. argentea seeds in presence and absence of GA (Results are given in progressive % seed germination)

Days	NH_4Cl							
	Light				Dark			
	1	2	3	4	1	2	3	4
GA alone (100 ppm)	18	19	23	26	18	22	25	29
GA + .05 M salt	14	26	29	29	12	28	31	35
GA + .1 M salt	27	45	51	54	24	37	44	48
Water	4	6	9	12	6	10	13	16
.05 M salt alone	6	8	10	14	6	14	14	20
.1 M salt alone	8	12	14	16	10	18	20	20

Days	NH_4SO_4							
	Light				Dark			
	1	2	3	4	1	2	3	4
GA alone (100 ppm)	18	19	23	26	18	22	25	29
GA + .05 M salt	18	24	26	26	18	23	26	28
GA + .1 M salt	26	36	38	38	28	38	40	42
Water	4	6	9	12	6	10	13	16
.05 M salt alone	4	6	8	14	7	13	17	20
.1 M salt alone	6	8	12	16	8	16	20	22

of 3% has been found to promote germination to the extent of 37% and 46% in light and dark, respectively (Figs 1, 2). Further increase in the concentration of thiourea exerts and inhibitory effect suggesting that the stimulatory effect of thiourea occurs only until the internal concentration of thiourea remains low (MAYER, 1956). Of all four compounds (thiourea, ascorbic acid, I. A. A. and GA) tried, thiourea has been found to be most potent in breaking the dormancy of *C. argentia* seeds, and I. A. A. is observed to reverse the negatively photoblastic nature of these seeds. GA renders these seeds insensitive to light.

Marked interaction between thiourea and ascorbic acid has been observed in the present investigation. Ascorbic acid at a sub-optimal concentration (10 mg %), not affecting germination alone under light incubation, has been found to markely increase the stimulation caused by thiourea (Fig. 3). This confirms the views of MAYBER and MAYER (1960) and VYAS and AGARWAL (1971). In the present investigation two roles of ascorbic acid have been observed: the synergism with thiourea in stimulating germination and as antagonist to

the stimulatory effect in light. Consequently, with an increase in concentration of ascorbic acid in an interaction with thiourea the per cent and rate of germination of these seeds have been found to decrease (Fig. 3). MAYBER and MAYER (1960) have obtained no interaction between thiourea and I. A. A. on germination of lettuce seeds. However in the present investigation a definite interaction has been observed at 10^{-8} and 10^{-9} M concentrations of I. A. A.

Of the four inorganic nitrogenous compounds tried, both KNO_3 and NH_4NO_3 have been found able to promote the germination of *C. argentea* seeds, as well as to accelerate the germination of these seeds promoted by GA (Table 1). These observations are in conformity with those of VYAS and GARG (1971). In the present case NH_4NO_3 has been observed to be more effective. NH_4Cl and $(NH_4)_2SO_4$, although by themselves very weak in inducing germination of *C. argentea*, are effective in enhancing the germination inducing activity of GA. Our observations confirm that nitrogenous compounds accelerate the physiological steps which can be influenced by GA (HASHIMOTO, 1961).

Acknowledgement

We are thankful to Professor H. D. KUMAR for providing facilities.

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RECENSIONES

STRASSBURGER, E.: Lehrbuch der Botanik. 30. Auflage, Stuttgart, Fischer Verlag, 1971. 842 Seiten

Es gibt wenig Lehrbücher, die eine 30. Auflage erreicht hätten. Ein solches ist jedenfalls das »Bonner Lehrbuch«, das erstmals im Jahr 1874 erschien. Ganzen Generationen diente es als Hilfsmittel des Studiums, acht Jahrzehnte hindurch. Das Werk wurde besonders dadurch wertvoll und unentbehrlich, dass es eine dem jeweiligen Stande der Wissenschaft gemäss Zusammenfassung der gesamten Botanik darbot, worin stets auch die neuesten Forschungsergebnisse eingebaut waren. Heute vermag aber ein einziges Handbuch diesen Anforderungen wohl kaum mehr Genüge zu leisten; es ist schwer, das Wissensgut der Botanik auf der Höhe der Zeit und im entsprechenden Umfang in einem Bande zusammenzufassen. Das ist auch dieser Arbeit anzumerken. Wenn auch der I. und II. Teil die Morphologie (miteinbegriffen Zytologie, morphologische Organisationsstufen, Histologie der Sprosspflanzen sowie Fortpflanzung und Vermehrung) und die Physiologie (einschliesslich Stoffwechsel, Wachstum und Vererbung sowie Bewegungsphysiologie), verglichen mit den analogen Teilen z. B. der 20. Auflage aus d. J. 1939 um etwa 100 Seiten stärker ist, kann man doch nicht behaupten, dass die Darstellung vollständig wäre, oder zumindest jedes — heute für wichtig erachtetes — Problem behandeln würde. So vermissen wir u. a. in der Zytologie die moderne Deutung und Erörterung der Totipotenz, der Kultur von Zellen, Geweben und Organen, und der Regeneration; in der Physiologie die ganze Regulationsproblematik (Zytokinine, Inhibitoren, Morphaktine, Retardanzien) überhaupt, bzw. die Darstellung ihrer genetischen Voraussetzungen und ihres Wirkungsmechanismus. Auch wäre eine etwas besser ausgeglichene Proportionierung des Materials angezeigt gewesen, da z. B. im Verhältnis zum Umfang der Wachstumsphysiologie (etwa 50 Seiten) die Physiologie der Bewegung (39 Seiten) etwas überdimensioniert erscheint, zumal auch die Physiologie des Wachstums zur Hälfte von der Genetik eingenommen wird. — Das Werk will den Bedürfnissen des zeitgemässen akademischen Unterrichts dienen und wurde deshalb 1971 von FREY—HAGEMANN—HALLER—HURDELBRINK durch eine sog. »Programmierte Studienhilfe« Botanik ergänzt, worin der ganze Stoff in 1551 Fragen u. Antworten aufgeschlüsselt ist. Die beiden Hauptteile Morphologie und Physiologie vermitteln in besonders ausführlicher Darstellung den klassischen Wissensstoff dieser Gebiete, aber auch in allem übrigen gebührt den Verfassern (D. DENFFER: Morphologie und W. SCHUHMACHER: Physiologie) die Anerkennung, Nützliches geleistet zu haben, indem Dozenten wie Studierenden die einzelnen Kapitel der Botanik in bündiger Fassung, aber auch anhand jüngster Erkenntnisse und Fakten dargeboten wird.

In der Jubiläumausgabe des Bonner Lehrbuches ist die Systematik und Evolution nicht nur von weit grösserem Umfang als die Morphologie und Physiologie, sondern auch um ein völlig neues, fundamentales Kapitel bereichert. Besonders die Samenpflanzen wurden mit grösster Gründlichkeit, nach modernster Auffassung, ganz »up to date« bearbeitet. MÄGDEFRAU suchte bereits in der früheren Ausgabe die Blütenlosen nach neueren Erkenntnissen darzustellen; im Gegensatz zu den ursprünglichen vier »Abteilungen« HARDERs führt er sechs ein, eigentlich noch immer von der hergebrachten morphologischen Basis ausgehend (*Schizophyta*, *Phycophyta*, *Mycophyta*, *Lichenes*, *Bryophyta* und *Pteridophyta*), was didaktisch zwar gerechtfertigt ist, dem heutigen Stand des entwicklungsgeschichtlichen Systems jedoch keineswegs entspricht, indem die 7 Klassen der *Phycophyta* und die *Myxophyta* als ein Stamm für sich anzusehen sind. Der Verfasser weist die Herleitung der Moose aus den Urfarnen von der Hand, wo doch dafür fossile Beweise vorliegen; auch der Stammbaum (S. 743) des anderen Verfasses

weist mit einer Seitenlinie in diese Richtung. Die Flechten sind phylogenetisch wohl kaum als eigenständig anzusehen, und wenn man noch weiter strafft, so könnte man eher die genetisch verwandten Pteridophyten und Spermatophyten gemeinsam in einer »Abteilung« zusammenfassen, vgl. die (älteren) Systeme von ZIMMERMANN und TAKHTAJAN. Die Grundlagen der Systematisierung hat EHRENDORFER aufs hervorragendste beschrieben. Die Kapitel sind: 1. Abstammungslehre und Evolutionsforschung, A. Die Beweise der Abstammungslehre; B. Ursachen der Variation (wie Ontogenie, Phänotyp und Genotyp, Mutationen, Rekombination und Vermehrung); C. Anpassung, Differenzierung und Divergenz (Selektion, genetischer Trend, Populationsstruktur; räumliche Isolation und Entstehung von Rassen; reproduktive Isolation und Artenentstehung); D. Mikro- und Makroevolution. 2. Systematik und Phylogenetik (mehrere Abschnitte); 3. Taxonomie und Nomenklatur. EHRENDORFER unterteilt die Divisio *Spermatophyta* in 3 Subdivisiones, wovon zwei die früheren Nacktsamigen bzw. die Klassen der *Coniferophytina* (*Ginkgoatae* und *Pinatae*) und der *Cycadophytina* (*Lyginopteridatae* — »*Pteridospermae*«, *Cycadatae*, *Bennettitatae* und *Gnetatae* — »*Chlamydospermae*«) sind, sowie die gewesenen Gedecktsamigen *Magnoliophytina*. In ihrer weiteren Einteilung folgt er dem System TAKHTAJANS (1966), doch mit seinen eigenen und mit CRONQUISTS (1968) Änderungen, indem innerhalb der Zweikeimblättrigen (*Magnoliatae*) 6, und innerhalb der Einkeimblättrigen (*Liliatae*) 3 Unterklassen unterschieden werden, mit zahlreichen »Überordnungen« und 72 Ordnungen. Meines Erachtens lassen sich diese Unterklassen oder Unterabteilungen nicht immer so scharf trennen; sie entsprechen vielmehr entwicklungsgeschichtlichen Reihen, wie z. B. in meinem System. Die Zufluchtnahme zu den sog. »Überordnungen« erschwert die Übersicht noch mehr — CRONQUIST verzichtet ja auch auf diese, und zu all dem kommt noch die neue Nomenklatur hinzu. (Diese steht übrigens mit den Grundsätzen des Code 1972 nicht im Einklang, da im Sinne der Recommandation 16 A bei den Stammpflanzen [*Cormophyta*] die Klassennamen nicht mit *-atae*, sondern mit *-psida* zu bilden sind. Von der didaktischen Seite her dürfte diese — phylogenetisch-systematisch wirklich sehr moderne, in einigen kleineren Fragen allerdings diskutable — Bearbeitung den Studierenden Übersicht und Erlernung des Systems der Samenpflanzen ziemlich erschweren. (In den früheren, allerdings tatsächlich überholten Systemen von FIRBAS zerfielen die Zweikeimblättrigen in 3 Gruppen und 35 Ordnungen, die Einkeimblättrigen in 11 Ordnungen.) Einige neuere wichtige chemotaxonomische Ergebnisse wurden aber nicht berücksichtigt (vgl. die neueren Publikationen von HEGNAUER, MEEUSE usw.). Trotz alldem ist das Werk EHRENDORFERS gewiss das modernste und wissenschaftlich solideste akademische Lehrbuch diesem Gebiet.* Es ist nur zu bedauern, dass die Pflanzengeographie (jetzt schon unter der Bezeichnung »Geobotanik«) im Bonner Lehrbuch auch weiterhin stiefmütterlich behandelt wurde (im ganzen 28 Seiten, was nur eine dürftige, skizzenhafte Darstellung bietet, besonders was die Pflanzengesellschaften anbelangt). Die äussere Ausstattung des Buches, sein Papier, das Illustrationsmaterial (viele neue Bilder) ist mustergültig; die farbigen Bilder der alten Ausgaben sind weggefallen. Der Preis (46 DM) ist dem angemessen, wenn auch für Studenten vielleicht etwas zu hoch.

M. MARÓTI—R. SOÓ

DR. B. M. MOELIONO: Cauline or Carpellary Placentation among Dicotyledons. I: The Cauline ovules of Centrosperms (text 1—292 pp); II: The Cauline ovules of Centrosperms (Plates: 1—92); van Corcum et Comp. N. V. Dr. H. J. Prakke et H. M. G. Prakke, Assen 1970.

The book, published in two volumes and containing 384 pages, discusses the cauline ovules of the *Centrospermae*, a part of the research studying the cauline or the carpel origin of placentation in Dicotyledons. The subject is highly interesting, it has been debated fairly often, and it is still timely.

The main text, the various statements, and the critique of literature (Vol. I) are complemented with microscopic drawings of accurate skill, and with morphologic-anatomical sketches relating to them (Vol. II). The text material is divided into five units, viz. Part I (1—141), Part II (145—199). Discussion (201—247), Summary (248—251), and the very extensive Bibliography (252—292).

Apart from general consideration, Part I of volume I reviews to lay the foundations of the examinations related to the ovary organization in some genera of the *Caryophyllaceae*,

* Auf die hier berührten neueren Systeme sowie auf die Modernisierung meines eigenen möchte ich — wenn mir dazu noch Zeit und Kraft bleiben — in einem besonderen Beitrag näher eingehen.

e.g. *Myosoton*, *Stellaria*, *Silene*, *Lychnis*, and the discussion of the results, in 12 chapters. Most of the latter divides into further units and submits a good survey of the elaboration of the theme and the problems posed. Chapters 1—5 introduces terminology, the interpretation of the carpellary leaf, nomenclature, placentation, and the "new morphologic-phylogenetical" conception then the exposition of the problem follows, along with some taxonomical questions, critical discussion of methods used by other authors, and the review of the author's material and methods. The subsequent four chapters (6—9) inform on his investigations, and observations, and the last three chapters (10—12) outline the aspects and inferences based on the results.

In the last analysis, the author emphasizes in Part I that the pistil of the *Caryophyllaceae* may be considered consisting of two parts, a so called abaxial area, congenitally coalescent from sterile phylla and a centrally situated, fertile, so-called axial region the latter, as a central placenta, may be further divided into two parts: "the placentae inferiores" and the "placenta superiores". Reference is also made, on a histogenetical basis, to the fact that the carpels, and the sterile septa respectively, fuse postgenitally with the fertile axial part (placentae superiores), and thus the placentation in the ovary of the *Caryophyllaceae* is merely "quasi-parietal". In addition the investigations concerned with this family covered also the conditions of formation of the vascular bundle system of the ovary and especially of that the central column. Two placental bundle systems develop in the central column of the various genera, one (axial) supplies for the ovules of the "placentae superiores", while the other (peripherial) those of the "placentae inferiores". Beside these results, characteristic ovule, and placentation reduction series could be demonstrated in the various tribes and genera within the family.

Part II of volume I discusses, while taking into consideration the results obtained for the *Caryophyllaceae*, the ovule organization, on a comparative morphological basis, of the following families: *Primulaceae*, *Portulacaceae*, *Basellaceae*, *Amaranthaceae*, *Polygonaceae*, *Nyctaginaceae*, *Phytolaccaceae*, *Aizoaceae*, *Mesembryanthemaceae*, *Cactaceae*, *Didireaceae*. In a number genera of the families (excepting the *Primulaceae*), some properties characteristic of the ovule organization in the *Caryophyllaceae* were recognizable (Chapters 13—23).

In the Discussion (24—27) typological considerations as well as the ovule organization of the *Centrospermae*, and within this the interpretation of the formation in placentation and vascular system on the one hand, the work and inferences of several researches (mainly of ZIMMERMANN) related to the results obtained on the other hand, and finally the evaluations of the author's own investigations are dealt with. The Summary emphasizes the essence of the results in well-structured divisions, in an exemplarily concrete cast.

Though volume II of the book lists only 76 Figures they consist of many (6—28) very demonstrative histological, and histogenetical section-drawings; they represent mostly 90×—350× magnifications, and support the inferences of the author satisfactorily.

In the last analysis, the conclusion of the two-volumes of investigations, results and discussions is that the parietal placentation described so far for the *Centrospermae* is actually "quasi-parietal", and that the ovules and their placentations are not of carpellary but a cauline origin, since the co-operation of the cauline tissues in the construction of the placental part of the central column was demonstrable with histogenetical methods.

S. SÁRKÁNY

STREET, H. E., COCKBURN, W.: Plant Metabolism. 2nd ed., Pergamon Press, Oxford—New York—Toronto—Sydney—Braunschweig, 1972. 321 pp.

One basis of reform in university education all over the world is the good text book. However, under the conditions of "production" in the new scientific results of our days, a text book up-to-date at its publication becomes out-of-date in one or two years. This danger increases when printing extends for a long period. Therefore textbooks of a high standard, covering only certain small areas, can now be published and even they need be frequently corrected and republished. Such a work is STREET and COCKBURN's Plant Metabolism, a multiply corrected, revised edition of the first 1963 publication. The new contribution is enlarged not only by some 5 printed sheets, but with a new chapter on Secundary Plant Products.

As regards the division in the book, it has a list of units, a list of abbreviations, author and subject indexes. It consists of nine chapters, titled 1. Introduction, 2. Cell Structure and Function, 3. Enzymes — The Catalysts of Metabolism, 4. Catabolism, 5. Anabolism, 6. Secondary Plant Products, 7. Absorption, Secretion and Translocation, 8. The Regulation of Metabolism, 9. Growth and Differentiation.

As is obvious from the contents, the work does not deal with the whole of plant anat-

omy, but only with a large part of it one might say, it discusses the developmental metabolism of the plant.

This work of a high standard has chosen its material fairly luckily, it does not neglect classical knowledge, but treats modern theories and recent results as well. The enormous information material is treated and ordered with restraint. The reader will form a clear conception of the beginnings, the development and the recent molecular biological level of our knowledge of plant development. It seems that the work provides an excellent basis for university teaching in plant physiology, but researchers working in the expert's field may find it useful as well, since the book provides a modern summary of the subject. English universities use this book as one of their textbooks. It is supplemented by 84 clear-cut figures, taken partly from studies published recently. The authors are professors in the University of Leicester. Their modern book of high standard should be at the disposal of all who are interested in either teaching or research in this special field, as well as on the shelves of special libraries. The lay-out is the same attractive form invariably produced by the Pergamon Press.

M. Maróti

Šestak, Z., Čatský, J. and Jarvis, P. G.: Plant Phytosynthetic Production—Manual of Methods. 1971, Dr. W. Junk N. V. Publishers, The Hague, 818 + xxi pp. 244 illustrations

The authors review in detail the most widely used methods — and the literature of the methods — in plant anatomical and ecological examinations of photosynthetic production. Among the 19 chapters, there are 9 (2—9 and 18) dealing with anatomical, and 4 (10—13) with ecological relevancies, while 6 chapters (l. 14—17 and 19) deal with related systems used in photosynthetic examinations, with the basic elements of physics and with measuring instruments.

Chapter 1 outlines the viewpoints in chosing the methods. The table containing the units occurring in the literature of photosynthetic production, as well as the symbols suggested for their denomination, promotes consistency in the interpretation of the results. The tabulatory survey of the factors limiting the photosynthetic intensity is an interesting attempt, but — in our opinion — it somehow simplifies the intricacy of the various factors.

Chapter 2 provides a comprehensive survey of gasometric methods — from the simplest to the most complicated ones.

Chapter 3 deals with the theoretical and instrumental problems of infra-red gas analysis, laying emphasis on the difficulties and correctional procedures occurring in carrying out the measurements in practice.

Chapter 4 describes the other, instrumentally simpler modifications in determining CO_2 concentration.

Chapter 5 presents the manometric methods.

Chapter 6 describes the construction of the microrespirometer and its application for measuring photosynthesis. This method is discussed by its own elaborator; no description in similar detail is available elsewhere in the literature.

Chapter 7 is less complete in discussing the applications of $^{14}CO_2$ in photosynthesis measurements. Probably, the authors considered it more reasonable to review the ample literature of the field.

Chapter 8, dealing with the methods of measuring light absorption, is brief also topically. Discussion of the role of peroxysomata should have been given room here.

Chapter 9 demonstrates the method of longterm experiments carried out on excised leaf pieces. It is a fairly interesting example of showing how much accuracy is needed in exactly carrying out an apparently simple method. It is reasonable to consider the viewpoints brought forward here also in short-term experiments with excised leaves.

Chapters 10 and 11 give a survey of the indices by which the productivity of the photosynthetic apparatus can be characterized (LAI, LAR, etc.).

Chapters 12 provides a literary survey of the measuring methods for radiation conditions prevailing in plant stands; Chapter 13 the micrometeorological procedures following the changes in CO_2 concentration.

Chapter 14 gives a detailed guidance for the determination of the surface of plant organs, in many cases of complicated form.

Chapter 15 is a tabulatory list of the special literature dealing with methods suitable for the determination of the size of stoma.

Chapter 16 deals with the CO_2 diffusion in leaf tissue and inside the plant stands, while Chapter 17 describes the methods for measuring the temperature of the leaves.

Chapter 18 gives a concise critical summary of the methods for chlorophyll determination.

Chapter 19 describes the instruments and the principal considerations applied when measuring radiating energy.

The book is amply illustrated. Block sketches are at critical points completed by original photographs.

The 36 authors of the manual are active and outstanding specialists of the various subjects. Accordingly, the methods are critically discussed, satisfying the requirements of researches working in the field of experiments.

In all probability, the book will prove useful for researchers working in the field of experimental ecology and photosynthesis. It will become a manual used on a large scale

Ágnes Faludi-Dániel

Jakucs, P.: Dynamische Verbindung der Wälder und Rasen. (Quantitative und qualitative Untersuchungen über die synökologischen, phytozönologischen, und strukturellen Verhältnisse der Waldsäume.) Akadémiai Kiadó, Budapest, 1972. 228 Seiten, 78 Tabellen, 41 Abbildungen und 16 Lichtbilder

Der Verfasser, der sich seit knapp 20 Jahren mit den Fragen der Karstbuschwälder befasst, hat dieses Werk den grundsätzlichen Problemen der Buschwaldforschung gewidmet, indem er die theoretischen und methodologischen Fragen der Erforschung der aus einem Mosaik von Wald- und Rasenflecken bestehenden Vegetationseinheiten behandelt. Im Mittelpunkt seiner Untersuchungen steht die Problematik der Waldsäume. Die Fragestellungen des Buches sind: 1. gibt es den Waldsaum als selbständige Vegetationseinheit überhaupt; 2. welche strukturellen, ökologischen, floristischen und zönologischen Eigenschaften besitzt der Waldsaum; 3. was sind die objektiven und realen Ansätze für eine zönosystematische Einordnung der Waldsäume; 4. welche Rolle spielt das Sprosslager beim Zustandekommen des Waldsaumes, und andererseits, was ist die Rolle des Waldsaumes in der Dynamik der Vegetation? — Um diese Fragen zu beantworten, untersuchte der Verfasser wiederholt und im Laufe von mehreren Jahren auf Musterflächen, die er an zwei Stellen des Transdanubischen Mittelgebirges ausgewählt hatte, Kontaktassoziationsserien von je 5 Bioeinheiten Steinrasen— Waldsaum—Mantel—Buschwald—Hochwald). Das erste Kapitel beschreibt die physischen Verhältnisse der Modellgebiete im allgemeinen, wobei einige auf Grund von Luftaufnahmen angefertigte Vegetationskarten benützt wurden. Das 2. Kapitel behandelt die in 4 Bioeinheiten durchgeführten Untersuchungen, u. zw. in 3 Teile gegliedert. Im ersten Teil (2.1) werden nach einigen kurzen Gedanken über die Methodik, sowie in Begleitung zahlreicher Originalabbildungen die Ergebnisse der Mikroklimamessungen dargelegt. Im dritten Teil (2.3) findet man mit Zugrundelegung der ausgewerteten TWR-Indikatoren eine synökologische Beschreibung der Bioeinheiten. In allen drei Teilen ist beachtenswert, dass der Verfasser — um jeglichen Subjektivismus in seinem Urteil zu vermeiden — die verschiedenen Methoden der statistischen Analyse (Varianzanalyse, D^2-Analyse, ferner χ^2-Analyse, lineare Regressionsanalyse) weitgehend anwendet, um das grosse Untersuchungsmaterial objektiv auszuwerten. Das dritte Kapitel behandelt die strukturellen und zönologischen Eigenschaften der Saumkomplexeinheiten, wobei die nach der Kleinquadrat-Methode gemachten Aufnahmen mit den Ähnlichkeitskoeffizienten ausgewertet wurden. Im vierten Kapitel findet man eine tiefschürfende phytozönologische Untersuchung der Bioeinheiten des Saumkomplexes; anhand einiger tausend zönologischer Aufnahmen werden die Kennarten der Assoziationsklasse *Trifolio-Geranietea* vom Verfasser kritisch überprüft. Dieses Kapitel bietet ein hervorragendes Beispiel dafür, dass sich grössere phytozönologische Probleme nur dann hinreichend lösen lassen, wenn die betreffenden Gebiete in ihrem grössten Teil persönlich, nach einheitlichen Gesichtspunkten und Methoden untersucht werden, wie es der Verfasser eben getan hat. Ansonsten läuft man Gefahr, statt des Wesentlichen irgendeinen besonderen Aspekt der Erscheinung zu erfassen, was zu provinzieller Anschauungsweise führt. Der Verfasser kommt zu der Schlussfolgerung, dass die Existenz der Säume sowie ihre ökologische und dynamische Funktion keineswegs in Frage gestellt werden kann. Allerdings gehören sie — vermöge ihrer ökologischen Verhältnisse und zönologischen Zusammensetzung — zum integrierenden Teil der Buschwälder; ihre etwaige Auffassung als selbständige zönologische Einheit ist lediglich dort begründet, wo eine zu den Saum- und Mantelassoziationen gehörende Optimalgesellschaft überhaupt nicht mehr vorkommt. Eine höhere zönologische Rangstufe gebührt ihnen aber auch in einem solchen Fall nicht, weil ihre Charakterarten bloss von lokaler Bedeutung sind. Eben aus diesem Grunde

verwirft der Autor z. B. die Klasse *Trifolio-Geranietea*. Beachtenswert ist in diesem Zusammenhang seine These, bei der Aufstellung der zönologischen Einheiten höherer Ordnung gebühre den physiognomischen Merkmalen gegenüber der floristischen Zusammensetzung Vorzug. Damit spricht er sich eigentlich für das HUMBOLDTsche Leitprinzip der Vegetationsauffassung aus, das der Systematik der Tropenvegetation bis auf heute zugrunde liegt. Des weiteren schlägt der Verfasser vor, dass als Bestimmungsbasis der Charakterarten jenes zönologische Verhalten der Pflanzenarten für massgebend angesehen werden müsste, welches sie im Zentrum ihres Verbreitungsareals aufweisen.

Der Rezensent des hier besprochenen Buches kam bei seinen Untersuchungen über die östliche Waldsteppenzone zu dem Ergebnis, dass die Saumbildung eine gesetzmässige Begleiterscheinung des Mosaiks der unterschiedlich strukturierten Gesellschaften darstellt. Das makroklimatisch bestimmte Vegetationsmosaik ist (klimazonal) makromosaikartig, m. a. W. grosse Wald- und Steppenflecken wechseln einander ab, wogegen die entstandene Saumgesellschaft von verschwindender Ausdehnung ist. In den Grenzgebieten der Waldsteppenzone (Ungarn, Tschechoslowakei, Österreich) begegnet man zum grössten Teil bereits mesoklimatisch motivierten Mikromosaiken, in welchen die relative Bedeckung und Bedeutung des Saumes erheblich grösser ist. Weiter westwärts, in der Zone der mesophilen Laubwälder kommt es nur mehr unter dem Einfluss von mikroklimatisch-edaphischen Faktoren zur Entstehung von Waldsteppen, zumal hier vornehmlich die Entstehung der Säume begünstigt wird. Parallel dazu verhalten sich die Waldsteppenkennarten (die sowohl auf den Steppenwiesen wie auch in xerothermen Eichenwäldern vorkommen) von Ost nach West zuerst als Wald- und Saumkennarten, in Grenzfällen als ausschliessliche Saumcharakterarten. Im Buch selbst liefert Abb. 26 ein sehr anschauliches Bild davon.

Schon allein aus diesem Grunde dürfte die Auffassung des Autors unbedingt richtig sein, wonach bei Aufstellung der höheren zönologischen Einheiten gerade von den grossen Vegetationstypen und nicht von den Säumen auszugehen wäre. Es dürfte wohl niemand im Ernst annehmen, dass die Pflanzengesellschaften der submediterranen Flaumeichenzone oder der kontinentalen Waldsteppenzone als Bioeinheiten zu den rheinländischen Saumgesellschaften gehörten oder gar deren Ausstrahlungen wären. Der in der Zönologie immer mehr überhandnehmende Partikularismus, der — unter anderem — auch für die wahre »Deskriptionsflut« massenweise aufkommender, allerlei höherer zönologischer Einheiten verantwortlich ist, soll als ernste Warnung dienen: der Autor verficht mit vollem Recht eine Forderung der objektive Wissenschaftlichkeit, indem er betont, dass sich die Vegetation an keine Landesgrenzen hält!

Als besondere Verdienste sind dem Buch noch anzurechnen: die Exaktheit des Ausdrucks und Stils, der mustergültige Aufbau der einzelnen Kapitel, die genaue Abgrenzung der Streitfragen, d. h. die präzise Fragestellung in den vieldiskutierten Problemen, die klare Beweisführung, die kurze und bündige Zusammenfassung der Ergebnisse, ferner die Tabellen und die anschaulichen, meist erstmalig gebrachten Originalabbildungen. Es ist nur zu bedauern, dass die ansonsten guten Lichtbilder nicht zu entsprechender Geltung kommen. Den Text schliesst eine imposante Bibliographie ab. Das Buch dürfte das bisher vielseitigste und gründlichste Werk über die Problematik der Waldsäume sein; es enthält auch etliche Feststellungen von grundlegender Bedeutung und ist damit eine wichtige Bereicherung des internationalen Schrifttums der Phytozönologie und -ökologie.

A. BORHIDI

HARTMANN, F. K.—SCHNELLE, F.: Klimagrundlagen natürlicher Waldstufen und ihrer Waldgesellschaften in deutschen Mittelgebirgen. Gustav Fischer Verlag, Stuttgart, 1970. 176 Seiten, 106 Abbildungen und 11 Tabellen

Es handelt sich um den vierten Band einer Buchreihe »Ökologie der Wälder und Landschaften«, der mit Überspringung des in Vorbereitung befindlichen 2. und 3. Bandes früher zu Herausgabe kam. (Den ersten Band hatte, ebenfalls in dieser Zeitschrift, **14**:445. 1968. R. Soó besprochen.) Ausser den beiden Autoren trugen noch E. FRANKEN, H. M MOLL und M. SCHNEIDER, mit der Auswertung und Interpretation des überaus grossen Beobachtungsmaterials zum Gelingen dieses Werkes bei. Das Buch gliedert sich in fünf Hauptabschnitte. Im ersten werden die Untersuchungsziele, organisatorischen Probleme, die allgemeinen Züge des Beobachtungsnetzes und die rechentechnischen Methoden der Datenauswertung behandelt. Dieses Kapitel ist ein besonders wertvoller Teil der Arbeit, da es in knapper Form, mittels anschaulicher Profildiagramme und hervorragender Vegetationskarten die synökologische Charakteristik von vier deutschen Gebirgsgegenden (Harz, Rhön, Nordschwarzwald, Pfalzer Wald) bietet. Im zweiten

Kapitel werden die klimatischen Eigenschaften der deutschen Mittelgebirge besprochen, vornehmlich auf Grund der Mittel- und Extremwerte von vieljährigen Beobachtungen im Material der »Klimakunde des Deutschen Reiches«. Es wäre hier wohl erwünscht gewesen, zusätzlich noch eine komplexe Auswertung der gesamten Veränderungen der einzelnen Klimaelemente und dadurch auch über das klimatische Gesamtbild einige Aufschlüsse zu bieten (durch Klimastudien oder Klimadiagramme) sowie einige Erscheinungen der Höhenzonation in ein besseres Licht zurücken. Es wäre auch nicht uninteressant gewesen, die statistische Häufigkeit bestimmter klimatischer Erscheinungen oder Faktoren zu untersuchen, weil man dadurch oft mehr Informationen erhält als durch die Mittelwerte. Das dritte Kapitel hat die Bestand- und Bodenklimaverhältnisse der untersuchten Berggegenden zum Gegenstand, während im vierten Kapitel die Auswirkungen der Relief- und Expositionsverhältnisse sowie noch einiger lokalklimatischer Gegebenheiten zusammengefasst sind. Der fünfte Teil enthält phänologisches Vergleichsmaterial, und macht als solches in botanischer, vegetationsgenetischer und produktionsbiologischer Hinsicht den wertvollsten Teil des Buches aus. Das ganze Werk kann bei der Planung von vergleichenden Makro- und Bestandklimauntersuchungen als Muster dienen und mit dem breitesten Interesse von Ökologen und Forstingenieuren rechnen.

A. Borhidis

Nagy, Eszter: Palynological elaborations of the Miocene layers of the Mecsek Mountain Annales of the Hungarian Geological Institute, Vol. LII, Fasc. 2, pp 1—420, Plates I—LVI 1969, Budapest

The elaborations constitute a paleobotanical summary. The whole text is in English, except for the 53 pages of introduction and the chapters on geology and methodology, and the one analyzing spore-pollen spectra. These are in Hungarian.

The importance of the elaborations lies in the fact that they furnish a description and paleobotanical evaluation of a Miocene basic flora which — by utilizing the boreholes put down in the course of geological surveys and excavations — submits the whole vertical section and horizontal range of Neogene layers of the Mecsek Mountains.

Part I: Causes and conditions of palynological investigations into the Neogene layers of the Mecsek Mountains.

Part II: Stratigraphic position of the specimens.

Part III: Method of investigation.

Part IV: This is the most important chapter of the work; a taxonomic description of 398 species (162 new) of 184 genera (45 new) from the phyla *Pyrrophyta*, *Chrysophyta*, *Chlorophyta*, *Mycophyta*, *Bryophyta*, *Pteridophyta*, *Gymnospermae* and *Angiospermae*.

Part V: Analysis of spore-pollen spectra. Its geological importance is that by investigating the spore-pollen of the basic flora it reconstructs the palaeobotanical picture of Neogene evolutionary regions lying around the paleozoic and mesozoic block of the Mecsek Mountains; by the flora type thus established the conditions of palaeogeography, palaeoclimatology and of sedimentation are clarified.

Four vegetation types have been established from the spore-pollen assemblage: marsh forest, galery forest and copse, mixed deciduous forest, hillside coniferous forest and mixed coniferous deciduous forest. Placing those of the vegetation types which are near in a geological age and in facies side by side in pictures, the study demonstrates that all of them are the deposit assemblages of a subtropical vegetation which testifies on the presence of a central massif. Palaeogeographical and floral affinity connections of the deposit assemblages are also stated. The results of investigations are of direct value by the paleoecological and percentage diagrams of the borehole logs and of the spore-pollen spectra.

Paleoclimate is shown in diagrams on the basis of the percentage distribution of floral elements according to temperature requirement and in the geological sequence of time of the layers.

Clear-cut photographs showing the basic flora, sketches in the text on the new species, as well as a subject index and a bibliography including also the latest references contribute to the fact that the author's work is valuable for all research workers, well utilizable in practice.

Márta Hajós

M. LUCKNER: Secondary Metabolism in Plants and Animals. 404 pages, 331 figures. Chapman and Hall Ltd. London, 1972.

The first edition of the work was in German in 1969; the new edition appeared also in English.

There are rather few comprehensive books on the products of secondary metabolism and their connections with primary metabolism; the available material consists usually of collected symposium lectures or deals with one or more groups of natural substances. They all lack a survey of the entire field in question. One of the greatest values of LUCKNER's book is this very survey with a claim to completeness. If a certain, though unbiassed, concentration is still perceptible in the content, it is to the advantage of secondary metabolic products evolving from the amino acids, and of the alkaloids, respectively. However, this is no fault, because a lack appearing in recent literature is thereby eliminated.

The material can be divided into two parts. Points A, B, C of the section comprising pages 1—54 is an introduction into secondary metabolism, both in the plant and animal kingdoms, specializing down to the cellular organels (pages A 1—12).

This is followed by a short summary (pages B 12—24) of the most important methods applied in the investigation of secondary metabolism, as e.g. isotopes, mutants and homogenizates, and enzymes. Concerning these latter, detailed discussions are submitted in the next part (pages C 25—54). I consider this chapter especially valuable because there is hardly any work of this scope able to afford place, beyond its strict subject matter, to methodical problems.

The presentation of the physical and chemical constants of the innumerable compounds cannot be proposed, only that of the biogenetical connexions. However, this, too, requires the introduction of very many structural formulae and series of formulae — and all of them are consistently treated by the modern stereochemical illustration. In many places, the mechanism of reactions is also indicated. Each chapter closes with a list of literature references. The presentation requires a preliminary experience in chemics and biochemics.

Part D, the essence of the work, discusses under the title "The biosynthesis and metabolism of secondary products of plant or animal origin" the structure, transformation and breakdown of every important natural compound. Classification is made, by the use of decimal symbols of three members, in 21 main groups, into which the compound-groups are relegated on the ground of their relationship to primary metabolism. The main groups deal, in the order of sequence, with the secondary products, whose points of origin are carbohydrates, various acids, activated izoprene, acids of a cyclic structure; groups 7—20 treat the syntheses starting from the amino acids, while main group 21 discusses the peptid and protein derivates originating as secondary products.

The richness of the content could be characterized only by a detailed presentation. The table of contents and the precise index afford easy orientation in a subject hitherto hardly surveyable owing to the rapid development of the field in the last ten years. And this requirement becomes daily more pressing. Research workers in botany, zoology, biochemistry, chemistry, pharmaceutics and agriculture demand works which present a serviceable picture of this field of science and special pointers to the latest literature in its branches.

This demand is met on the highest level by LUCKNER's excellent work.

P. NÁNÁSI

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ACTA BOTANICA

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РЕЗЮМЕ

ДЕЙСТВИЕ ИНТЕНСИВНОСТИ СВЕТА НА ПРОИЗВОДСТВО СУХОГО ВЕЩЕСТВА И ПОТРЕБЛЕНИЕ ЭНЕРГИИ В РАСТЕНИЯХ ТОМАТА

СУДХИР РАНЬЯН БАРООВА и И. ХОРВАТ

В обоих исследовавшихся сортах сухой вес линарно уменьшился при повышении интенсивности затенения. Уменьшение было более значительным у растений сорта Kecskeméti konzerv, чем у растений сорта Kecskeméti törpe. В полевых, а также в контролированных условиях в обоих сортах параллельно повышению интенсивности света наблюдается увеличение концентрации общих карбогидратов. В противоположность этому концентрация азота снижается. Понижение интенсивности света посредством затенения в общем привело к понижению потребления энергии. На изменение световых отношений два сорта томата реагируют различным образом.

АНАТОМИЧЕСКИЕ И ФОТОСИНТЕТИЧЕСКИЕ РЕАКЦИИ ЛИСТЬЕВ QUERCUS PUBESCENS WILLD. НА ФАКТОРЫ СРЕДЫ В РАЗЛИЧНЫХ ЭКОСИСТЕМАХ II. ФОТОСИНТЕТИЧЕСКАЯ АКТИВНОСТЬ

Г. ФЕКЕТЕ, Й. СУЙКО-ЛАЦА и Г. ХОРВАТ

Авторы изучали способность листьев к инкорпорации CO_2, с учетом анатомических свойств листьев (при интенсивности света в 10 000 люкс и благоприятных условиях водоснабжения) на теневых листьях деревьев *Quercus pubescens*, растущих на четырех различных местах произрастания, при комбинации 2 уровней водоснабжения и освещения. На четырех местах произрастания в качестве образца выбрали по 3 дерева. Результаты вариационного анализа инкорпорации CO_2 листьями отобранных деревьев, растущих на различных местах произрастания, в 5% случаев оказались достоверными, а при разбивке на отдельные факторы, влияние света в 1% случаев оказалось достоверным. Показатели запаса древесины отобранных деревьев находятся в противоречии с данными способности листьев инкорпорировать CO_2. На продукцию запаса древесины влияет количество воды, всасываемой из почвы.

Авторы искали связь между анатомическими признаками и количеством осваиваемой двуокиси углерода и нашли, что между соотношением палисадной/губчатой паренхимы и инкорпорацией $CO_2/dm^2/h$ наблюдается 1%-ая достоверная корреляция, и между размером клеток мезофилла, так наз. межклеточным соотношением и инкорпорацией CO_2 имеется 0,1%-ая связь. При проведении Path-анализа авторы выявили, что среди анатомических признаков, принятых во внимание при исследовании, межклеточное соотношение листьев оказывает наибольшее влияние на вариабильность количества инкорпорированной двуокиси углерода, и меньше всего сказывается влияние соотношения палисадно-губчатого слоя паренхимы. Полученные результаты действительны в условиях примененной авторами системы исследования.

НОВЫЙ РОД ОТКРЫТОСЕМЕННЫХ ИЗ ТРИАСОВЫХ (БАССЕЙН ДЖОНДУАНА) ЯРУСОВ ТИКИ, МАДХЬЯ ПРАДЕШ, ИНДИЯ

Х. К. ГОСВАМИ

В работе дается описание ископаемых открытосеменных растений, отнесенных к новому роду ***Tikioxylon***, собранных из триасовых ярусов Тики, Южная Рева. ***Tikioxylon*** характеризуется спиральными утолщениями и араукальными углублениями на стенке трахеид. Два вида ***T. hughesii*** и ***T. spiralli*** показывают различия в отношении годичных колец, **cross field pits** и сердцевинных лучей.

ИЗУЧЕНИЕ РАЗВИТИЯ АДВЕНТИВНОГО ЗАРОДЫША, ОРГАНИЗОВАВШЕГОСЯ ИЗ КЛЕТКИ КАЛЛЮСА DAUCUS CAROTA L. В РАННЕЙ ФАЗЕ ЭМБРИОГЕНЕЗА

Л. ХЕСКИ

Автором был изучен адвентивный эмбриогенезис в культурах каллюса корней ***Daucus carota*** L., выращенных на питательной среде RM—1964, дополненной 0,02 и 1,00 ppm кинетина и 2 ppm индолуксусной кислоты. Согласно результатам наблюдений, эмбриогенез эмбриоидов, развивающихся из ставших зародышевыми клеток каллюса, соответствует развитию находящихся в проэмбриональной несколькоклеточной стадии, зародышей, развивающихся из зигот.

УЛЬТРАСТРУКТУРНОЕ ИССЛЕДОВАНИЕ ИСКОПАЕМЫХ СПОР ПАПОРОТНИКООБРАЗНЫХ И ПЫЛЬЦЕВЫХ ЗЕРЕН ГОЛОСЕМЯННЫХ

М. КЕДВЕШ и А. ПАРДУЦ

Авторами было проведено ультраструктурное исследование ископаемых спор папоротникообразных и пыльцевых зерен голосемянных. В результате работы были сделаны следующие заключения. В ультраструктуре стенки споры изоспоровых папоротников нижнего эоцена и верхнего мела (***Leiotriletes adriennis*** **asp.** ***triplanoid***, ***Toroisporis*** [***Toroisporis***] ***eocenicus***, ***Appendicisporites tricuspidatus***, ***Microfoveolatosporis pseudodentatus***) нельзя выявить хорошо определяемых слоев. На экзоспории, в первую очередь на основе электрондеиза, можно обособить два главных слоя (эктекзоспорий и эндекзоспорий). На ***Spheripollenites scabratus*** из юрского периода была установлена ультраструктура экзины типа покрытосемянных. Ультраструктура стенки спор **cf.** ***Araucariacites*** или ***Granulatisporites*** **fsp.** имеет характер покрытосемянных. Формы рода ***Classopollis*** и ***Classoidites*** можно хорошо отдифференцировать на основе ультраструктуры слоя колумеллы над эндэксиной.

РЕГУЛИРОВАНИЕ ИНДОЛУКСУСНОКИСЛОЙ ОКСИДАЗЫ В ГЕНЕТИЧЕСКИ ОПУХОЛЕВЫХ И НОРМАЛЬНЫХ РАСТЕНИЯХ ТАБАКА И В ИХ ТКАНЕВЫХ КУЛЬТУРАХ

Э. И. КОВАЧ и П. МАЛИГА

Авторы изучали функцию системы индолуксуснокислой оксидазы — полифенола в растениях сорта **Nicotiana alata**, **N. glauca**, **N. Langsdorffii**, в гибридах **N. alata** × **N. langsdorffii** $\mathbf{F_1}$, в туморообразующих гибридах **N. glauca** × **N. Langsdorffii** $\mathbf{F_1}$ и в тканевых культурах нормальных и опухолевых генотипов. В стеблях активность индолуксуснокислой оксидазы была более высокой, чем в листьях. В противоположность

этому содержание хлорогеновой кислоты было более низким в стеблях, чем в листьях. В генетических опухолях активность индолуксуснокислой оксидазы была высокой, и содержание хлорогеновой кислоты было низким. В исследованных тканевых культурах наблюдалась высокая активность индолуксуснокислой оксидазы и низкое содержание хлорогеновой кислоты. В изучаемых сортах табака, в гибридах, в тканях нормальных и опухолевых генотипов физиологическая регуляция нормальна. Однако генетическая регуляция играет более важную роль в образовании генетических опухолей. Между геномами существует взаимодействие различной доминанции. Данные авторов доказывают также гомологию стеблей и генетических опухолей.

ИЗУЧЕНИЕ УСЛОВИЙ ЗОНАЛЬНОСТИ И ПРОДУКЦИИ НА ПОЙМЕ РЕКИ ДРАВЫ I. НАПОЛНЕНИЕ БОЛОТ И ЗОНАЛЬНОСТЬ ПОЧВЫ И РАСТИТЕЛЬНОСТИ В ПОЙМЕ РЕКИ ДРАВЫ

М. КОВАЧ и И. КАРПАТИ

Анализуется процесс наполнения болот и зональность почвы и растительности в пойме реки Дравы. В болотах и их пограничной зоне в соответствии с условиями воды и влажности формируются три типа почв (пойменная луговая почва, болотная луговая почва и болотная почва). Соответственно условиям почвы и воды формируется зональное распределение растительности. Для краевой зоны болот характерна минералогенная серия сукцессии, заканчивающаяся рощевым лесом, а для их средней зоны — органогенная серия сукцессии, заканчивающаяся лесным болотом. Почвы различных растительных зон показывают достоверные отклонения в отношении ряда физических и химических факторов.

АНАТОМИЯ СОЦВЕТИЯ И МОРФОЛОГИЯ ЦВЕТКОВ AMARANTHUS LEUCOCARPUS S. WATS

К. Т. СЕБАСТИАН и Б. Д. ДЕСПАНДЕ

У растений *Amaranthus leucarpus* цветки располагаются в форме дихазиального соцветия с регулярным уменьшением числа цветков в отдельных метелках. В одной метелке максимальным числом цветков является девять, и редукция происходит от семи до пяти цветков, в конце имеется три цветка, которые являются тремя центральными цветками трех дихазиев.

ДОПОЛНЕНИЕ К СТАТЬЕ «ВИДЫ И ПОДВИДЫ РОДА OPHRYS»

Р. ШОО

На основе новейших литературных данных (прежде всего **Sundermann** 1970 и **O. et E. Danesch** 1972) и письменных сообщений дается дополнение к работе **Species and Subspecies of the Genus Ophrys** 1970. Автор во многих случаях подвергает критике утверждения вышеуказанных авторов, в частности новые таксоны, выдвинутые **O. et E Danesch**. В обозрении даются обозначенные порядковым номером названия видов **Ophry agg.**, под ними названия «малых видов» (**small species**) и переходных форм (**transitus**).

СОВРЕМЕННАЯ ТАКСОНОМИЯ ГРУППЫ FFSTUCA OVINA

Р. ШОО

В работе дается современная критическая разработка венгерских таксонов видовой группы *Festuca ovina*. Обсуждаются следующие виды и таксоны и их инфраспецифические единицы: *F. ovina* agg.: *F. ovina* s. str., *F. tenuifolia*, *F. cinerea* agg., сюда относятся еще: *F. pallens*, *F. vaginata* agg.: *F. vaginata*, *F.* × *stricta* (*pallens* × *rupicola*), *F.* × *wagneri*

предположительно *vaginata* × *rupicola*), *F. valesiaca* agg.: *F. dalmatica*, *F. pseudodalmatica*, *F. valesiaca*, *F. rupicola* (*«F. sulcata»*), *F. pseudovina*. Первая глава содержит цитотаксономические данные *F. ovina* 14 (сообщено 28—70), *F. tenuifolia* 14, *F. pallens*: 14 !, 28 !, 42 !, *F. vaginata*: 14 !, *F. stricta*; ?, *F. wagneri*: 28 !, *F. dalmatica*: 28 !, 48—49 (?), *F. pseudodalmatica*: 28 !, *F. valesiaca*: 14 !, 28 !, *F. rupicola* 14, 28, 42 !, *F. pseudovina*: 41 !, 28 ! (знаком! обозначены проконтролированные венгерские данные). Во второй части работы дается ключ для определения видов и высших форм, а в третьей главе сообщается обзор всех принимаемых в соображение таксонов группы *F. ovina*. Новой комбинацией является только *F. arenicola* (Prod.) Soó. В примечаниях и в дополнении даются критические замечания к работам Beldie et Horánszky et al. (1972). Автор придерживается того мнения, что классификация видов группы *F. ovina* возможна только на основе анатомо-биометрических показателей; цитотаксономические данные до сих пор не предоставляют надежных результатов, их приходится дополнить точными анализами кариотипов (как напр. в отдельных французских, чехословацких и польских работах), а для определения видов сомнительного происхождения необходимо провести современные цитогенетические исследования. Полезны также биометрические анализы популяций.

ЛИЯНИЕ ЧИСЛА СПОР, ПРИХОДЯЩИХСЯ НА ЕДИНИЦУ ПОВЕРХНОСТИ ПЛОТНОЙ ПИТАТЕЛЬНОЙ СРЕДЫ НА ХОД ПРОРАСТАНИЯ СПОР У НЕСКОЛЬКИХ ВИДОВ ASPERGILLUS

(Предварительное сообщение)

Я. А. ТОТ

Автор изучал действие различной густоты посева конидий *Aspergillus flavus*, *A. nidulans* и *A. niger* на динамику процента прорастания на агаре Цапек Докса. Экспериментальные данные показывают, что в густых посевах по сравнению с редкими посевами проявляется стимулирующее действие на всхожесть. Ответственным за это явление по всей вероятности следует считать накопление в питательной среде стимулирующих прорастание веществ.

ИЗМЕНЕНИЯ СОСТАВА АЛКАЛОИДОВ В МЛЕЧНОМ СОКЕ, НАБЛЮДАЕМЫЕ В ТЕЧЕНИЕ СУТОК

Д. ВАГУЙФАЛВИ

На основе изучения 10 особей от каждого из трех штаммов мака было установлено, что содержание алкалоидов в млечном соке показывает в течение суток значительные изменения, причем с различным характером изменений у отдельных растений. Около полудня и после полуночи, как общеее количество алкалоидов, так и соотношение отдельных оснований обнаруживают характерное изменение. Поэтому эти сроки можно рассматривать как суточные поворотные точки обмена алкалоидов, происходящего в млечном соке мака.

Значительные качественные и количественные индивидуальные различия, проявляющиеся в суточном колебании содержания алкалоидов в млечном соке мака, доказывают, что только на основе обособленного изучения отдельных растений можно выяснить фактические условия изменений, происходящих внутри растения, как напр. изменений суточной периодичности.

Изучение 30 растений *Papaver orientalis* также подкрепляют выводы, сделанные в связи с исследованием мака.

ДЕЙСТВИЕ АУКСИНА НА РОСТ И ОБМЕН ВЕЩЕСТВ СТЕРИЛЬНОГО, ИЗОЛИРОВАННОГО КАЛЛУСА ТАБАКА

Й. ВЕТТЕР

Ауксин (β-индолил-уксусная кислота = ИУК) является одним из самых важных регуляторов роста растительных клеток и тканей. Поэтому было выбрано тема, тесно связана с этими процессами. Автор работал методом стерильного выращивания, сохранял

культуру стеблевого каллуса табака на основной питательной среде без ауксина, и на основных средах, содержащих разные количества фитогормона. После определенного инкубационного времени (это время было 34 дня или 50 дней) мы оценили количественные изменения разных параметров, возникнутые влиянием ауксина. При оценке было определено рост веса, т. е. свежий вес (мг/день), сухой вес (в процентах свежего веса), число клеток ($\times 10^6$/г свежего веса), вес клеток ($\times 10^{-4}$ мг/клетка), содержание белок (мг/г свежего веса), содержание рибонуклеиновых кислот (μг/г свежего веса; и μг/г сухого веса), активности ферментов рибонуклеазы [OD_{260}], пероксидазы [изменение OD_{420}/г свежего веса/мин.], ауксин оксидазы [μг окисляющегося ауксина/г свежего веса/час]. На основе наших результатов можно установить:

1. Рост тканей табака зависит от концентрации ауксина по оптимальному графику; максимальный рост был индуктирован концентрацией 0,25—1,00 мг/л.

2. Была корреляция между ростом культур — выращиванных 34 дня или 50 дней — и испытанной, низкой активностью рибонуклеазы. Активность хорошо растущих вариантов явилась низкой, и торможение роста причинило высокую активность. Эти изменения можно наблюдать уже после кратковременной инкубации.

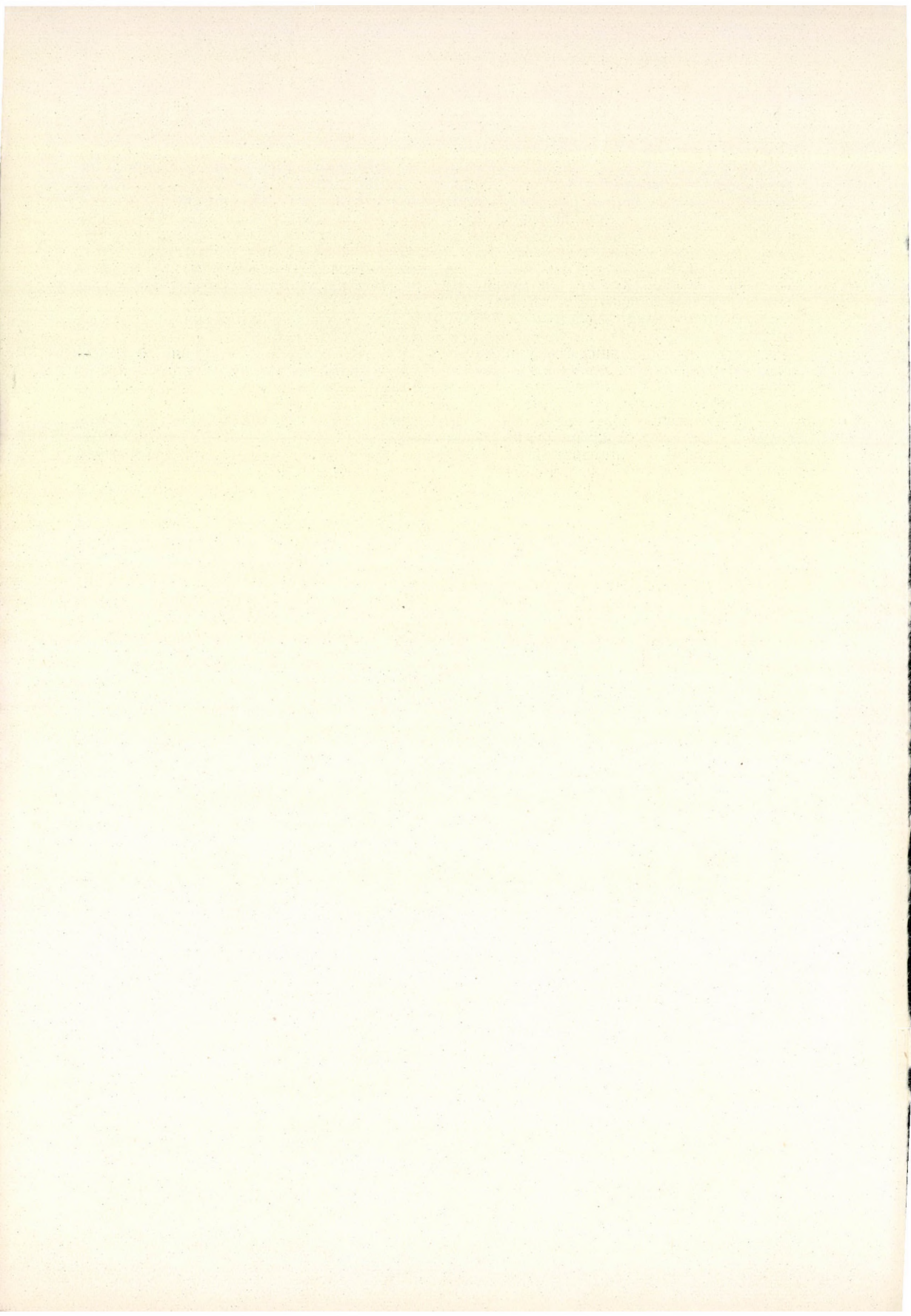
3. Из данных содержаний РНК и белок следует, что действие ауксина — и в этом случае — охватит эти параметры обмена веществ.

4. Изменения активностей пероксидазы и ауксиноксидазы показали взаимосвязь между этими ферментами. Возможно, что осуществляется единая — состоящая из нескольких изоферментов — система фарментов, и эта выполняет функцию пероксидазы и ауксин оксидазы.

Наши данные укрепляют возможную, регуляторную роль рибонуклеазы в процессах роста. С другой стороны метод стерильного выращивания тканей является полезным для исследований физиологии растений.

ИЗУЧЕНИЕ ДЕЙСТВИЯ ТИОУРЕИ, ИНДОЛУКСУСНОЙ КИСЛОТЫ И ГИБЕРЕЛЛИНОВОЙ КИСЛОТЫ НА ПРОРАСТАНИЯ СЕМЯН CELOSIA ARGENTEA L., НАХОДЯЩИХСЯ В СТАДИИ ПОКОЯ

Л. Н. ВИАС и Р. Л. ШРИМАЛ

После 60-недельного хранения в сухом помещении семена *Celosia argentea* оказались в состояния покоя. На свету 3%-й раствор тиоуреи повышает прорастание семян на 33%. Взаимодействие тиоуреи (3%) и аскорбиновой кислоты (10 мг%) вызывает на свету максимальное прорастание (62%), в то время как при инкубации в темноте максимальную всхожесть (65%) можно достигнуть при взаимодействии гибереллиновой кислоты (100 ppm) и NH_4/NO_3 (1%). Аскорбиновая кислота вызывает два эффекта: первый — синергизм с раствором тиоуреи — стимулирует прорастанию, а другой вызывает на свету антагонистическое действие на стимуляторный эффект тиоуреи. Неорганические азотистые соединения катализируют стимулирующую активность гибереллиновой кислоты на прорастание.

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